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REVERSIBLE SEX-MUTANTS IN LYCHNIS DIOICA (WITH FIFTEEN FIGURES): *George Harrison Shull* - - -

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THE

BOTANICAL GAZETTE

NOVEMBER 1911

REVERSIBLE SEX-MUTANTS IN LYCHNIS DIOICA[1]

GEORGE HARRISON SHULL

(WITH FIFTEEN FIGURES)

Six hermaphrodite specimens of *Lychnis dioica* L. were found in cultures of 1908, and eight in 1909. With respect to their hereditary behavior in the first generation, when used as pollen parents, these hermaphrodites proved to be of two kinds, the individuals *A* and *B* being capable of determining the hermaphrodite character in their male offspring, while individuals *C* and *D* behaved exactly like normal males, giving progenies consisting of females and normal males.

The conclusion was reached (SHULL **26**) that the hermaphrodites are modified males, because (1) in all families in which the first mentioned type of hermaphrodite was used as the pollen parent the offspring consisted of females and hermaphrodites in the same ratio as would have been expected of females and males if a normal male had been used as the pollen parent, and because (2) the second type of hermaphrodite when used as a pollen parent gave the same result that a normal male would have given.

Accepting tentatively the Mendelian explanation of sex first clearly enunciated by CORRENS (**6**), which recognizes the one sex as homozygous and the other sex as heterozygous with respect to a sex-producing gene, it was decided that these hermaphrodites (and therefore also males) must be heterozygous, because (1) the males are capable of being modified in such manner as to display function-

[1] Read at the meeting of the Botanical Society of America, Minneapolis, December, 1910.

al organs of both sexes, and because (2) self-fertilized hermaphrodites produce dimorphic progenies, consisting of females and hermaphrodites.

In my first paper on the inheritance of sex in *Lychnis* (SHULL **26**), I represented the sex genes by the conventional signs for the sexes (♀, ♂, and ☿). As these signs were used in my tables with two different meanings—to represent sometimes the character of the genes and at other times the character of the soma—I suspect that readers may have experienced some difficulty in comprehending the tables. I shall therefore adopt here the plan usually followed by students of genetics, of representing the genes by letters, letting *Ff* be respectively the presence and absence of a female determiner, *Mm* a male determiner, and *Hh* a hermaphrodite determiner. The conventional signs for the sexes will be used in this paper only in their more usual signification, referring to the nature of the soma, that is, the sporophyte.

If CORRENS' view of sex determination is correct, and the males are heterozygous, the females must be homozygous. CASTLE (**5**) suggests that in such a case the females will always be *positive* homozygotes, having a pair of sex genes (*FF*) corresponding with a single equivalent gene (*Ff*) in the male. I do not believe that this view can be substantiated, as there seems no good reason why females should not be negative homozygotes in some plants and animals, "neutral" homozygotes in others, and positive homozygotes in a third class. If the females are positive homozygotes, the somatic formula of the two sexes may be represented thus: *FF*=♀, and *Ff*=♂; if the females are negative homozygotes, the corresponding symbols will be *FFmm*=♀, and *FFMm*=♂; and if the female is a "neutral" homozygote, the formulae of the two sexes will be *FF*=♀, and *FM*=♂. Only the first two of these assumptions concerning the nature of the females were considered in my earlier paper, and either was found capable of explaining the results secured in the first generation, provided the presence of a partially independent hermaphrodite factor (*H*) might also be assumed.

Whether there was any genetic relationship between the hermaphrodites *A* and *B* which produced hermaphrodite offspring, and *C* and *D* which produced males, could not be determined in the first

generation, and two explanations seemed possible: (1) these two types of hermaphrodites might be respectively homozygous and heterozygous in regard to a modifying factor *H*, whose presence was assumed, on the suggestion of CORRENS, as possibly necessary for the change of a normal male into a hermaphrodite; (2) the hermaphrodites of the second type (*C* and *D*), which gave first generation progenies equivalent to those produced by normal males, might owe their hermaphrodite character to some accident of development which affected the soma alone, leaving the germ cells unchanged. In this case they might be appropriately called "somatic hermaphrodites," to distinguish them from those of the first type (*A* and *B*) which transmitted the hermaphrodite character to their male offspring and which are therefore to be recognized as "genetic hermaphrodites" or true hermaphrodite mutants.

Neither the character of the females nor the relationship of the two types of hermaphrodites could be determined from the results of the first generation, but it was obvious that at least a partial solution could be expected from the second generation. To attain this end a large number of crosses were made in 1909, by using hermaphrodite individuals and their derivatives in various combinations with each other, with unrelated females, and with normal males. The offspring of these crosses were grown during the summer of 1910, and the 104 families produced from them included 6132 individuals which came to bloom and of which the sex was recorded. These records were made in the writer's absence by Mr. R. CATLIN ROSE, to whose energy, faithfulness, and care it gives me pleasure to testify.

In order to comprehend fully the problems involved, it will be advantageous to consider some assumptions which were permitted by the results of the F_1 crosses, and whose availability is partially tested in the F_2 families reported in the present paper. In this connection it is also important to consider briefly the "presence and absence" hypothesis, a full discussion of which, however, would require too great a digression. Although this so-called hypothesis is frequently referred to by students of genetics, I am not aware that it has ever had a very definite formulation, and it would undoubtedly be defined differently by different students.

"Presence and absence" came into use in the first place, simply as a convenient method of expression to avoid the confusion which arises when the same dominant character is described as an alternative of several different characters which are hypostatic to it, and which may themselves be present or absent in any particular instance. The very general applicability of this mode of expression naturally suggested to various writers (HURST **18**, SHULL **27**, etc.) that it might have a more fundamental significance than merely as a convenient form of description. These authors considered it simpler and more practical to suppose that the heterozygous genes are unpaired, and that the "*absence*" of a character[2] is unrepresented by any internal unit corresponding with the gene which determines the "*presence*" of that character. The "presence and absence" hypothesis need not be associated, however, with the conception of unpaired determiners in the heterozygote, for in any *pair* of organs there may be present a function or feature in one member of the pair which is absent in the other member, or both members may be alike in kind but different in quantity or activity, the differential between the two being in this case the determiner of the alternative characters involved. This excess in one member of the pair would be present, of course, in that member only, and must be absent in its mate. Whether the hypothesis of unpaired genes or that of paired genes represents the true condition in any particular instance, and whether the absence of a character is absolute or only relative, will not interfere in the least with the use of "presence and absence" as the most convenient method of stating a great majority of the alternative characters with which the student of heredity has to deal. For the application of these different phases of the "presence and absence" hypothesis to the sex problem in *Lychnis*, attention is directed to the following table:

[2] It is to be regretted that some writers have misconstrued the meaning attached by most geneticists to the expression "absence of a character." The absence of the Angora character in cats, rabbits, etc., does not result in a hairless animal, but one with short hair. In *Oenothera* the absence of *rubricalyx* pigmentation does not prevent the production of anthocyan in the amount and localization characteristic of *O. rubrinervis* (see GATES, R. R., Studies on the variability and heritability of pigmentation in *Oenothera*. Zeitsch. Ind. Abst. Vererb. **4**:337–372. 1911).

TABLE I

PRIMARY ASSUMPTION I.—There is a separate factor *H* which changes the male to a hermaphrodite, but which cannot find expression in the female.

SECONDARY ASSUMPTION I.—The two types of hermaphrodite are respectively homozygous and heterozygous in the factor *H*.

WHEN THE FEMALE IS	FORMULAE		REQUIRED ASSUMPTION	HYPOTHETICAL COMBINATIONS	EMPIRICAL RESULTS	REMARKS
	female	hermaphrodite				
Positive, and						
H homozygous	*FFhh*	*FfHH*	.....	*FFHh* and *FfHh*	♀ and ☿	
H heterozygous	*FFhh*	*FfHh*	*H* coupled with *F* in heterozygote	*FFHh* and *Ffhh*	♀ and ♂	
Negative, and						The correctness of these assumptions would result in: F_1 ♀'s with latent *H* F_1 ♀'s unlike P_1 ☿'s.
H homozygous	*FFmmhh*	*FFMmHH*	.....	*FFmmHh* and *FFMmHh*	♀ and ☿	
H heterozygous	*FFmmhh*	*FFMmHh*	*H* allelomorphic to *M* in heterozygote	*FFmmHh* and *FFMmhh*	♀ and ♂	
Neutral, and						
H homozygous	*FFhh*	*FMHH*	.....	*FFHh* and *FMHh*	♀ and ☿	
H heterozygous	*FFhh*	*FMHh*	*H* coupled with *F* in heterozygote	*FFHh* and *FMhh*	♀ and ♂	

TABLE I—*Continued*

SECONDARY ASSUMPTION II.—The second type of hermaphrodite is purely somatic and unrelated to the first type, and the first type is then heterozygous in respect to *H*.*

WHEN THE FEMALE IS	FORMULAE		REQUIRED ASSUMPTION	HYPOTHETICAL COMBINATIONS	EMPIRICAL RESULTS	REMARKS
	female	hermaphrodite				
Positive, and						
Genes unpaired	*FFhh*	*FfHh*	*H* allelomorphic to *F*	*FFhh* and *FfHh*	♀ and ☿	♀'s cannot transmit hermaphroditism
Genes paired ..	*FFhh*	*FfHh*	*H* coupled with *f*			
Negative.....	*FFmmhh*	*FFMmHh*	*H* coupled with *M*	*FFmmhh* and *FFMmHh*	♀ and ☿	
Neutral.....	*FFhh*	*FMHh*	*H* coupled with *M*	*FFhh* and *FMHh*	♀ and ☿	F_1☿'s are like P_1☿'s

PRIMARY ASSUMPTION II.—There is no factor *H*, hermaphroditism being caused by a mutative modification of the sex gene, which may then be represented by M_H, F_H, or f_H.

Positive, and						
Genes unpaired	*FF*	F_Hf	.....	None that could result in	♀ and ☿	The ♀ cannot be positive unless *F* has a synaptic mate
Genes paired ..	*FF*	Ff_H	Chance distribution	*FF* and Ff_H	♀ and ☿	
Negative.....	*FFmm*	FFM_Hm		*FFmm* and $FFMm_H$	♀ and ☿	♀'s cannot transmit hermaphroditism
Neutral.....	*FF*	FM_H		*FF* and FM_H	♀ and ☿	F_1☿'s same as P_1☿'s

* The case in which *H* is homozygous in the genetic hermaphrodites has been already tabulated under secondary assumption I.

Particular attention should be given to only two points in this table until after the results secured in the second generation have been considered. The assumptions which form the basis of the first section of the table lead to the expectation (*a*) that females derived from hermaphrodite families, whether they be fertilized by normal males or by their hermaphrodite sibs, will yield families in which the male offspring are hermaphrodite and normal male in equal numbers; and (*b*) that the hermaphrodites of the second generation when used to fertilize females from normal male families will produce no hermaphrodites, but only females and males. The alternative assumptions involved in the second and third sections of the table, on the other hand, lead to the expectation that, regardless of the origin of the female, no hermaphrodites will be produced normally, except when fertilization is brought about by sperms from a genetic hermaphrodite, and then the result will always be the same whether this hermaphrodite was a mutant or whether it was derived from an antecedent hermaphrodite.

We may now proceed to examine the results of the crosses. This will be most easily accomplished by considering each type of cross separately in the following fourteen cases. In the model pedigrees, illustrated under each case, the oldest ancestors entered in the diagrams are females and males both of which came from normal families, whose matings had been controlled during at least three still earlier generations, and which are known to have been in each such previous generation the result of crosses between females and normal males, and to have belonged to families in which no hermaphrodite mutants appeared. In the diagrams all male and hermaphrodite individuals which appeared as mutants are indicated as such, and it should be understood that any male or hermaphrodite not so marked was a member of a family which consisted of a normal proportion of its own type, that is, either male or hermaphrodite.

CASE I

Crosses of genetic hermaphrodite mutants with females

Only 2 of the 8 plants recorded as hermaphrodites in 1909, in otherwise normal male families, were successfully used for breeding. One of these, bred to 2 different unrelated females, produced 72

females and 88 hermaphrodites (nos. 09123 and 09171). The other, bred to the same 2 females, produced 116 females and 53 hermaphrodites (nos. 09124 and 09172). The result of these four crosses, involving 2 hermaphrodite mutants, was therefore 188 females and 141 hermaphrodites, thus showing that these 2 hermaphrodite mutants were of the same character as the two denomi-

Pedigree no.	Result	Pedigree no.	Result
0869	58♀:36☿:1♂	08150	59♀:43☿
08106	53♀:50☿	09123	36♀:53☿
08118	60♀:40☿:1♂	09124	52♀:30☿
08127	51♀:52☿	09171	36♀:35☿
08128	50♀:51☿	09172	64♀:23☿
08149	67♀:33☿	Total	586♀:446☿:2♂

nated *A* and *B* in my earlier report. For the sake of completeness, the crosses of *A* and *B* already reported are included in the tabulation of these crosses, the total progeny from this type of cross being 586 females, 446 hermaphrodites, and 2 males.

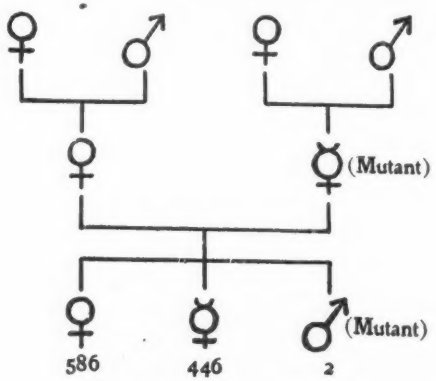

FIG. 1.—Model pedigree for case I

Two other individuals, which had a derangement of the sexual characters of such a nature that the lobes of the calyx were transformed into stigmas, and in one instance a small ovary with apparently functional stigmas was present in the center of the flower and

associated with functional stamens, were of such anomalous character that they have not been included among the 8 recognized hermaphrodites found in normal families in 1909, but they will be mentioned later under case XIII in connection with the somatic hermaphrodites *C* and *D* of my preliminary report.

CASE II

WHEN GENETIC HERMAPHRODITE MUTANTS ARE SELF-FERTILIZED

Pedigree no.	Result
08115	24♀: 19♀
08117	9♀: 6♀
08119	110♀: 95♀
Total	143♀:120♀

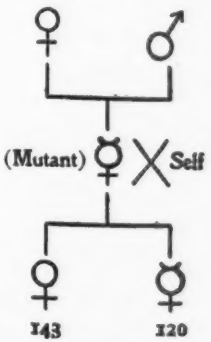

FIG. 2.—Model pedigree for case II.

None of the new hermaphrodite mutants discovered in 1909 were successfully self-fertilized, and the pedigrees here reported are repeated from my former paper for the sake of completeness. All the self-fertilized hermaphrodites which yielded progenies in my 1910 cultures belonged to a later generation, being offspring of a self-fertilized hermaphrodite and not the progeny of new mutants. They consequently belong to a separate case and will be considered next. The agreement of these results with those under case I leads to the conclusion that the eggs of the hermaphrodite are all of one type, that is, female-bearing, like those of the females. The significance of this result will be considered later.

CASE III

WHEN F_1 HERMAPHRODITES ARE SELF-FERTILIZED

Pedigree no.	Result	Pedigree no.	Result
09185	5♀: 8♀	09217	16♀: 9♀
09186	17♀: 6♀	09218	17♀: 1♂
09187	18♀:23♀	09219	22♀: 5♀
09191	6♀:10♀:1♂	09220	2♀: 2♀
09216	1♀	09222	43♀:38♀:1♂
		Total	147♀:101♀:3♂

The first four of these families were produced by self-fertilizing 4 individuals of pedigree number 08115, and the rest by self-fertilizing 6 individuals of number 08119. Most of these families were too small to show obvious differences in the genetic composition of the different parent plants, or between them and the hermaphrodite mutants tested under case II. The small size of the families is due to the comparatively poor development of the ovaries and stigmas in most hermaphrodites, and the consequent difficulty of securing large quantities of seeds by self-fertilization. Most of the attempts to self-fertilize the hermaphrodites resulted in failure, and only in a small proportion were any seeds produced. The total result agrees with results secured from the observation of larger families, and it is fair to assume that the relatively large differences shown by some of these families are not significant because of the smallness of the progenies. This conclusion will be fully justified I believe, when it is observed under case IV that the very same plants, which produced the somewhat variable progenies shown above, gave uniform results when they were crossed with an unrelated female.

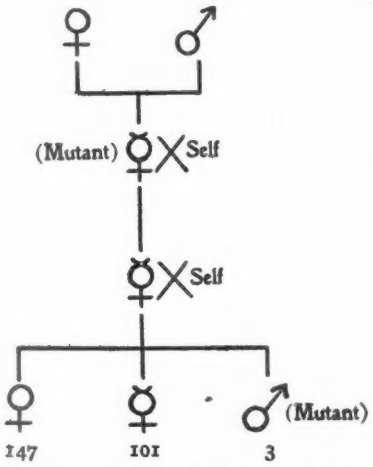

FIG. 3.—Model pedigree for case III

CASE IV

WHEN HERMAPHRODITES FROM THE PROGENY OF A SELF-FERTILIZED HERMAPHRODITE MUTANT ARE CROSSED WITH AN UNRELATED FEMALE

The families 09133 to 09142, inclusive, resulted from pollinating different flowers of a single female, 08114(4), with the pollen from 10 different hermaphrodites taken consecutively in family 08115, and the remaining 19 families were produced by pollinating the same female, 08114(4), with pollen from 19 different hermaphrodites

in family 08119. This series of experiments, like those under case III, was calculated to discover any genetic differences which

Pedigree no.	Result	Pedigree no.	Result
09133	44♀:20♀:1♂	09154	57♀:26♀
09134	55♀:27♀	09155	48♀:42♀
09135	41♀:37♀	09156	54♀:41♀
09136	42♀:31♀	09157	56♀:32♀
09137	47♀:33♀	09158	59♀:25♀
09138	47♀:37♀	09159	51♀:29♀
09139	50♀:29♀	09160	43♀:29♀
09140	65♀:25♀	09161	52♀:29♀
09141	38♀:34♀	09162	25♀:30♀
09142	51♀:40♀	09163	56♀:33♀
09149	52♀:25♀:1♂	09164	16♀:14♀
09150	49♀:30♀	09165	46♀:40♀
09151	51♀:45♀	09166	36♀:19♀
09152	66♀:24♀:1♂	09167	36♀:19♀
09153	49♀:22♀	Total	1382♀:867♀:3♂

might exist among F_2 hermaphrodites, and the fact that these 29 different individuals when crossed with a single female produced

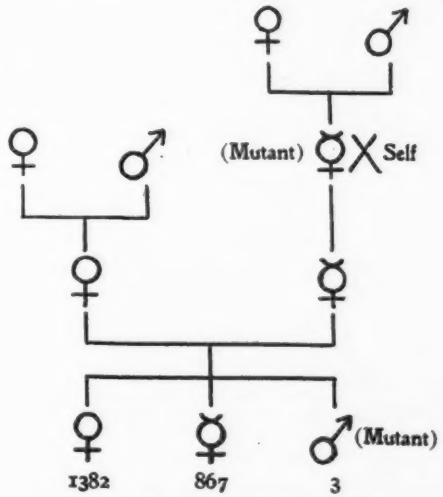

FIG. 4.—Model pedigree for case IV

essentially identical results leads to the conclusion that no such genetic differences existed. This conclusion is apparently open to

but one criticism; the characters of the female chosen to be the mother of all these families might dominate such different characters as were possessed by the hermaphrodites, in which case all families would show identical composition regardless of the variations in the pollen parents. This suggested dominating influence of the female is rendered untenable, however, by the fact that the same female was pollinated by 7 other hermaphrodites having different histories from those considered under the present case, and also by 11 different males of diverse origin, and in every case the males among the progenies were of the same type as their pollen parent.

CASE V

WHEN FEMALE OFFSPRING OF SELF-FERTILIZED HERMAPHRODITES ARE CROSSED WITH AN UNRELATED MALE

Pedigree no.	Result	Pedigree no.	Result
09174	21♀: 8♂	09190	49♀: 22♂
09176	50♀:34♂	09193	28♀: 25♂:1☿
09178	34♀:20♂:1☿	09196	33♀: 23♂
09180	39♀:11♂	09198	58♀: 34♂
09182	36♀:17♂	09200	26♀: 22♂
09184	42♀:34♂:2☿	09202	22♀: 17♂
09189	12♀: 6♂	09204	21♀: 32♂
		Total	471♀:305♂:4☿

These families were produced by pollinating 14 different females, taken consecutively in 08115, with pollen from a single normal male, 0855(36), in an unrelated family. The essentially equal results of all these crosses indicate that there are no differences among these females which were not dominated by the sex character of the pollen parent. As this pollen parent was a male from a normal male parentage, it may be appropriately assumed to have been free from any hypothetically possible hermaphrodite modifier *H*. If such a modifier had been possessed by any of these 14 females, a more striking evidence of that fact should be presented than is found in the occurrence of less than 1 per cent of hermaphrodite individuals among the offspring. This is a smaller percentage of hermaphrodites than has been found in one or two cases among the offspring of a female pollinated by a normal male, neither

parent having had any hermaphrodite connections. It appears fair, therefore, to consider these four hermaphrodites simply as mutants, and not as genetic derivatives from their maternal grandfather. The few hermaphrodites occurring in the families included under the present case may be related to the fact, however, that the females belong to a hermaphrodite family, for the same male 0855(36) was crossed with seven other females and with one hermaphrodite, and among the 443 offspring produced there were no other hermaphrodites.

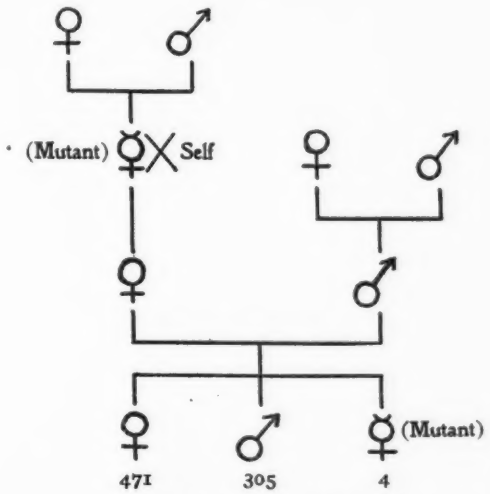

FIG. 5.—Model pedigree for case V

Allowing for the same frequency of occurrence of hermaphrodites as shown in the table above, there should have appeared among these 443 individuals derived from the same male crossed with other females at least two hermaphrodite mutants. This number is so small that they may possibly have been omitted through the errors of random sampling, but the suggestion may be made that while a female cannot transmit hermaphroditism to its offspring, it may perhaps supply an intracellular environment favorable to the mutation of the male genes into hermaphrodite genes.

CASE VI

WHEN THE DAUGHTERS OF A SELF-FERTILIZED HERMAPHRODITE ARE CROSSED WITH ONE OF THEIR HERMAPHRODITE SIBS

Pedigree no.	Result	Pedigree no.	Result
09173	6♀: 2♂	09192	9♀: 2♂
09175	23♀:13♂	09195	39♀:17♂
09177	32♀:17♂	09197	48♀: 6♂
09179	45♀:28♂	09199	40♀:20♂
09181	63♀:16♂	09201	40♀: 7♂
09183	4♀: 3♂	09203	35♀:10♂
09188	36♀: 7♂	09205	9♀: 7♂
		Total	429♀:155♂

The seed parents of these families were the same 14 females which produced the families considered under case V. In the present case they were all pollinated by a single hermaphrodite, 08115(9), in the family to which they themselves belonged. The results correspond closely with those of the last section, except that in this case the males were invariably hermaphrodites, showing as before that the character of the pollen parent determines the sex character of the male offspring. It may be noted that most of these families contained a strikingly high percentage of females, as compared with those under case V, there being 73.46 per cent of females among the progenies of case VI, and only 60.7 per cent among those of case V. The meaning of such differences in the sex ratios is quite unknown at the present time, and no discussion of the series of experiments which are in progress for the purpose of finding an interpretation of such variable ratios will be undertaken here. It is believed, however, that the question of the sex-ratios constitutes an altogether different problem, and has no direct bearing upon matters relative to the genetic interrelationships of the different sexual types, which are alone under consideration in this paper.

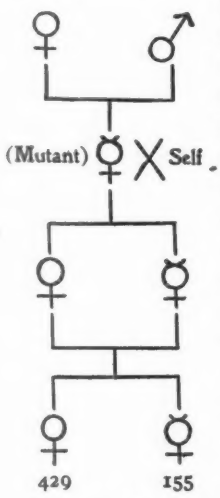

FIG. 6.—Model pedigree for case VI.

CASE VII

WHEN HERMAPHRODITE OFFSPRING OF AN OUT-CROSSED HERMAPHRODITE MUTANT ARE CROSSED WITH UNRELATED FEMALES

Pedigree no.	Result	Pedigree no.	Result
09112	36♀:18☿:1♂	09118	46♀:42☿
09113	56♀:31☿	09145	46♀:49☿
09114	7♀: 3☿	09146	50♀:39☿
09115	20♀:14☿	09148	55♀:24☿
09116	39♀:26☿	09260	26♀:27☿
09117	47♀:19☿	Total	428♀:292☿:1♂

These families are essentially similar in nature to those considered under case IV, except that in the present case the mutant was crossed with an unrelated female instead of being self-fertilized. The first 7 of these families were produced by crossing 7 different

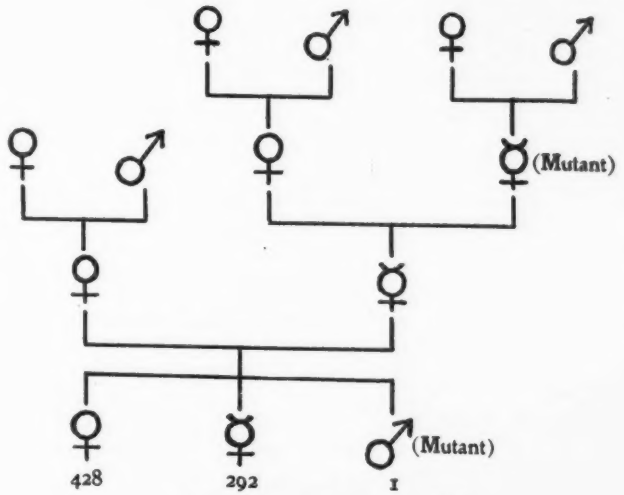

FIG. 7.—Model pedigree for case VII

hermaphrodites in 08118, upon a single female, 08109(1); the next three (09145–09148) were the result of using three of the same hermaphrodite individuals in the pollination of the female, 08114(4), which was used as the seed parent of all the families included under

case IV. The genetic equivalence of the different hermaphrodites again stands out clearly in these results, and when the ratios of the two series are compared, it is found that the percentage of hermaphrodites produced by the hermaphrodite offspring of a self-fertilized hermaphrodite is slightly lower than that produced by the offspring of these cross-bred hermaphrodites, the former producing only 38.2 per cent of hermaphrodites and the latter 42.6 per cent. The difference is too small to be of significance, particularly in view of the fact that much wider differences than this are found in families produced from different seed capsules on a single plant when pollinated by a single male. It might have been expected, perhaps, that a self-fertilized hermaphrodite would have produced a larger percentage of hermaphrodites than would be produced by the same hermaphrodite crossed upon a female of a normal family. The fact that such a result does not appear is further proof that, although the hermaphrodite is a heterozygote, its egg cells are of a single type and like those of the normal females.

The last family under this section was produced by crossing a hermaphrodite of 08128(16) upon a female in a genotypically distinct strain of *Lychnis dioica*, received several years ago from the vicinity of Harrisburg, Pennsylvania. The result is quite the same as in the other families, all of which were derived from a common stock secured at Cold Spring Harbor, Long Island.

CASE VIII

WHEN HERMAPHRODITES ARE POLLINATED BY NORMAL MALES

Pedigree no.	Result
08116	21♀: 11♂: 2☿
09215	8♀: 1♂
Total	29♀: 12♂: 2☿

I have already remarked the difficulties encountered in the use of hermaphrodites as self-fertilized seed parents. The difficulties are still greater when the problem requires the crossing of the hermaphrodites with other males, for nearly all the numerous castrations which have been made have resulted in the dropping

of the flowers without further development. Only one family (08116) was produced in 1909 from a cross of this kind. It was

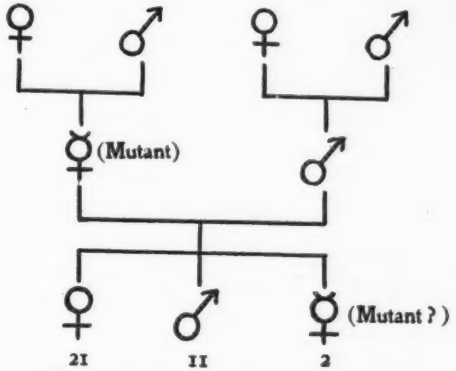

FIG. 8.—First model pedigree for case VIII

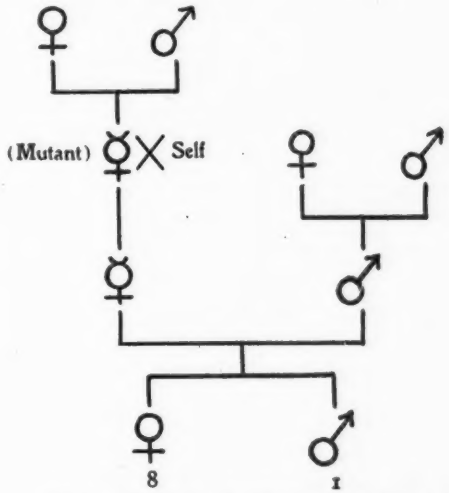

FIG. 9.—Second model pedigree for case VIII

reported upon in my preliminary paper, and is repeated here. The occurrence of two hermaphrodites in this small family suggested that the hermaphrodite character might be inherited from the

mother as well as the father. On this account the cross between hermaphrodites and males must be considered the most important of all combinations in interpreting the relations of the sexes. The difficulty involved in the castration of the flowers permits the question whether the two hermaphrodites may not have been due to a faulty technique, for males produced from unintentional self-pollinations would be hermaphrodites.[3] Special efforts were put forth in 1909 to secure more crosses of this character, but these resulted in a single success, and that of so limited extent as to be wholly indecisive. The 9 offspring of this cross (09215) consisted of 8 females and 1 male, so that the little evidence which such a small family can give is in harmony with the proposition that the character of the female parent has no influence upon the sex characters of the male offspring, except possibly by supplying an intracellular environment which is favorable or unfavorable to the occurrence of sex mutation, suggested under case V. Continued efforts are being made to secure more data from combinations of hermaphrodites with normal males.

CASE IX

WHEN HERMAPHRODITE OFFSPRING OF A HERMAPHRODITE MOTHER AND NORMAL MALE FATHER ARE CROSSED UPON AN UNRELATED FEMALE

Pedigree no.	Result
09143	38♀:38♂
09144	51♀:33♂
Total	89♀:71♂

The appearance of 2 hermaphrodites in family 08116 of case VIII immediately raised the question whether they were true genetic hermaphrodites like *A* and *B*, or whether they might not be somatic hermaphrodites whose hermaphrodite character was not in any way related to the fact that they were the offspring of a hermaphrodite seed parent. If they should prove to be somatic

[3] In a family grown in 1911 from a cross between a white-flowered hermaphrodite and a homozygous blue-flowered male, all the offspring were blue-flowered and several (less than 6 per cent) were hermaphrodite, thus showing that such hermaphrodites are not in this instance due to any unintentional self-fertilization.

hermaphrodites, they would be in reality of the same genotype as their pollen parent, thus offering no exception to the general rule that the male parent determines the sexual type of its male offspring.

Both of these hermaphrodites were crossed upon female 08114(4), already mentioned in cases IV and VII. No influence of the male grandparent appears, as all of the male offspring in these two

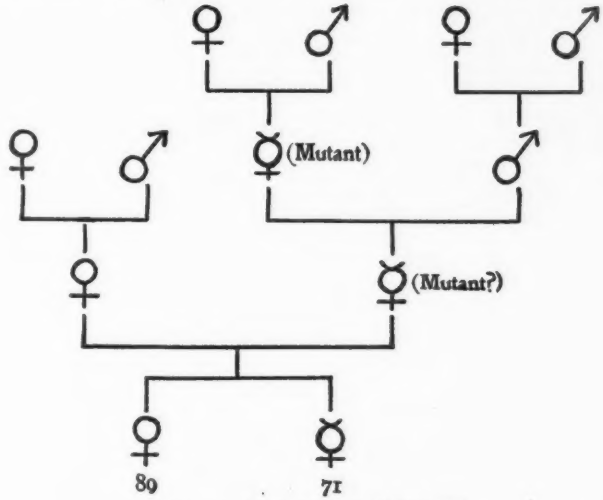

FIG. 10.—Model pedigree for case IX

families were hermaphrodites. This result proves that the 2 hermaphrodites of 08116 were genetic hermaphrodites. One of these hermaphrodites was also self-fertilized and gave a progeny of a single hermaphrodite, constituting family number 09210. It would be rash to draw a conclusion from a family consisting of a single individual, and nothing could have been derived from it if by chance that individual had been a female. The fact that it was hermaphrodite instead of normal male, however, confirms the conclusion that the hermaphrodite parent was a genetic hermaphrodite like its own seed parent.

Whether these two hermaphrodites owed their hermaphrodite character directly to their hermaphrodite mother, or whether it

resulted from a mutation of the male genes received from their father, cannot be definitely decided, but further experiments are in progress to test the possibility that the eggs of hermaphrodites can carry hermaphroditism and may therefore sometimes transmit it to their offspring. The evidence thus far is against their doing so to any considerable extent.

CASE X

CROSSES BETWEEN FEMALES AND THEIR HERMAPHRODITE SIBS IN A FAMILY PRODUCED BY CROSSING HERMAPHRODITE AND MALE

Pedigree no.	Result
09207	1♀: 1♂
09208	12♀: 9♀:1♂
09209	46♀:30♀:1♂
09211	36♀:17♂
09212	32♀:16♀
Total	127♀:73♂:2♂

These are crosses in which the same 2 hermaphrodites of 08116, discussed in case IX, were used as the pollen parents in crosses with

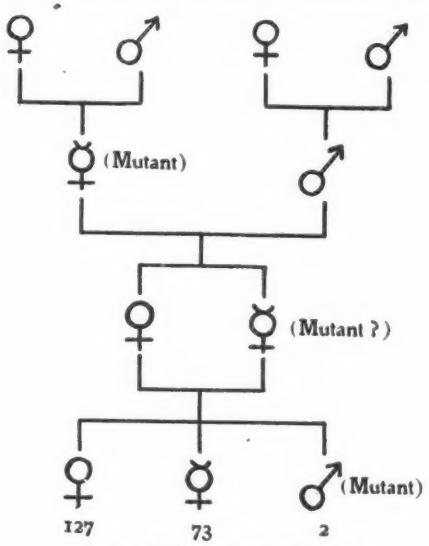

FIG. 11.—Model pedigree for case X

three different females in the same family. The results may be compared with those under case VI, where sib crosses were also dealt with. The comparison shows that the results were identical, though in one case the parents were the progeny of a self-fertilized hermaphrodite, while in the other the parents resulted from the cross of a hermaphrodite fertilized by a male. Thus is given still further evidence that these hermaphrodites in 08116 were genetic hermaphrodites and that such hermaphrodites are of like hereditary capacity, whatever their origin.

CASE XI

WHEN DAUGHTERS OF A FERMAPHRODITE MOTHER AND MALE FATHER ARE CROSSED WITH AN UNRELATED MALE

Pedigree no.	Result
09206	7♀: 5♂
09213	10♀: 8♂
09214	33♀: 21♂
Total	50♀: 34♂

The first of these families (09206) had the same seed parent as the first two families (09207 and 09208) under case X, and the

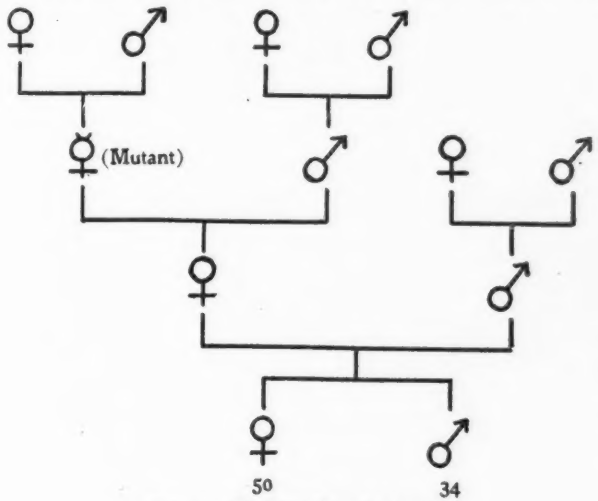

FIG. 12.—Model pedigree for case XI

second (09213) had the same seed parent as the last two families (09211 and 09212) under that case. The pollen parent in all three families of the present case was the same normal male, 0855(36), that was used for all the crosses in case V. It is consequently fair to assume that the differences in the result under case X and case XI are wholly referable to the male parent, and that such differences as appear between case X and case V are referable to the seed parents. There is no difference in the latter instance, while the fundamental difference in the former is that in case X the males were hermaphrodite, while in the present case they were normal males, thus showing again the correspondence between the male offspring and their pollen parent.

CASE XII

WHEN MALE MUTANTS ARE CROSSED WITH UNRELATED FEMALES

Pedigree no.	Result
09147	40♀:40♂
09239	43♀:44♂
Total	83♀:84♂

It will be recalled that among the 705 offspring produced in 1909 from crosses between females and the genetic hermaphrodites, *A* and *B*, there were 2 males and 305 hermaphrodites. In similar manner it will have been noted that in a number of the cultures of 1910 a very small percentage of such males have appeared in families of which the male offspring were generally hermaphrodite. Instances of this kind are noted above, under cases I, III, IV, V, VII, and X. Whether these males were true males or possibly somatically modified hermaphrodites may now be considered.

The families reported under the present case were produced by pollinating two different unrelated females with pollen of 08118(13), one of the two males derived from genetic hermaphrodite fathers in 1909. No hermaphrodites were produced, thus showing that the pollen parent was a true male, and not a hermaphrodite which had suffered the suppression of the female organs because of some purely somatic influence. The frequency of occurrence of such male mutants may be inferred from the fact

that 11 of them appeared among progenies comprising a total of 3331 females and 2126 hermaphrodites. In other words, they constitute about 0.2 per cent of the total progeny of the genetic hermaphrodites when the latter are used as pollen parents. In no single family did more than one such male mutant occur. While these numbers are too small to allow an accurate estimate of the

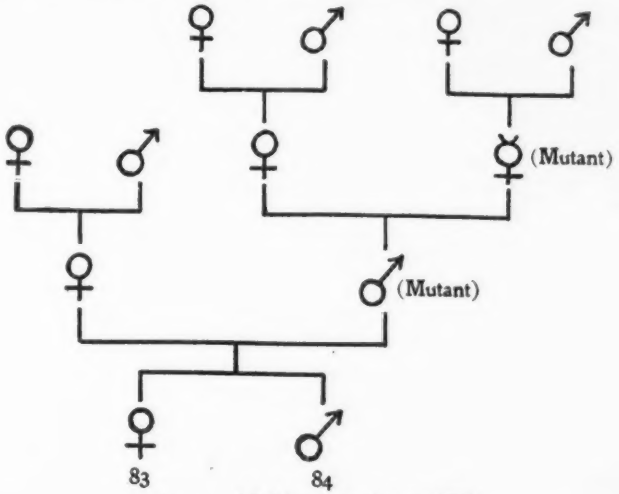

FIG. 13.—Model pedigree for case XII

relative frequency of hermaphrodite and male mutants, the evidence seems to indicate that there is no striking difference between the capacity of males to give rise to hermaphrodite mutants, and that of hermaphrodites to give rise to male mutants, though male mutants have appeared with slightly greater frequency than hermaphrodite mutants.

CASE XIII

WHEN SOMATIC HERMAPHRODITES ARE CROSSED WITH UNRELATED FEMALES

Pedigree no.	Result
08125	39♀:55♂
08132	26♀:18♂
0995	56♀:26♂
0996	63♀:34♂
Total	184♀:133♂

The pedigrees 08125 and 08132 are those of hermaphrodites *C* and *D* among the cultures of 1909, which were reported upon last year. If the "model pedigree" illustrated in the diagram (fig. 14) be compared with that under case I (fig. 1), the two will be seen to correspond perfectly. In fact, the hermaphrodites *A* and *B* included under case I were full sibs of hermaphrodites *C* and *D* whose progenies are repeated here. These 4 hermaphrodites which were found in the cultures of 1908 were indistinguishable

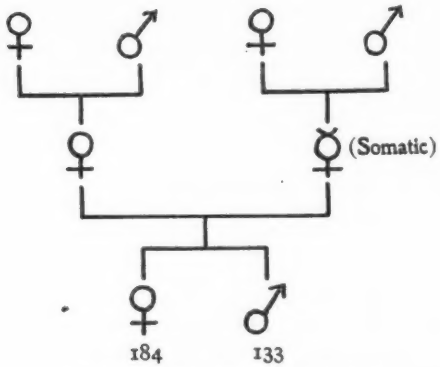

FIG. 14.—Model pedigree for case XIII

from one another in their external characters, and the fact that they belonged in two different categories was only demonstrated by the breeding tests.

No additional instances have been found in which a hermaphrodite indistinguishable from the usual type of "genetic hermaphrodites" has proved to be simply a somatic variation of the male. However, 2 peculiar variant individuals found in one family of the 1909 cultures exhibited an analogous behavior, and consequently their progenies have been added to those of *C* and *D* under this case. The 2 individuals used as pollen parents of the families 0995 and 0996 had several lobes of the calyx prolonged and modified to the form and structure of stigmas, and one of the flowers had in the center a small unicarpellary ovary with an apparently functional stigma. Both of these plants had func-

tional stamens, and both approached more nearly to the type of normal males as the season advanced. On account of the anomalous position of the stigmas in these plants, they are not to be included in the same class with the other hermaphrodites which have been considered, but it may not be unfair to accept the appearance of stigmatic calyx teeth in these male plants as additional evidence that the male is heterozygous in regard to sex, but normally has the presence of the female character completely hidden by the dominance of the male character. A somatic derangement may be assumed as the proximate cause of the appearance of the misplaced stigmas.

These 2 abnormal plants were crossed upon a female sib, 08109(1), and produced together 119 females and 60 normal males, not one of which showed any development of stigmatic calyx lobes or other female characteristics. The female 08109(1) was the one used in case VII for a number of crosses with genetic hermaphrodites, and it was also used as the seed parent in 20 crosses with males of various origin. In all of the other crosses upon this female, the males among the progenies were of the same type as the male parent used in the particular cross from which they sprang, thus showing that this female exerted no modifying influence upon the sex character of her male offspring. This makes it reasonable to conclude that the stigmatic calyx lobes were a purely somatic variation.

CASE XIV

THE SECOND GENERATION FROM A SOMATIC MALE

Pedigree no.	Result
09119	50♀:27♂
09120	37♀:16♂
09121	33♀:26♂
09122	61♀:14♂
09168	49♀:42♂
09169	45♀:10♂
09170	58♀:33♂
Total	333♀:168♂

In order to make sure that the conclusions drawn from the first generation regarding the character of the hermaphrodites *C* and *D*,

as discussed in case XII, were sound, and that there was not simply the temporary disappearance of the hermaphrodite character through some thinkable vagary of dominance in the F_1, 5 males in 08125 were tested in crosses with 2 different females. The resultant progenies consisted of 333 females and 168 males. Not a single hermaphrodite appeared, thus convincingly supporting

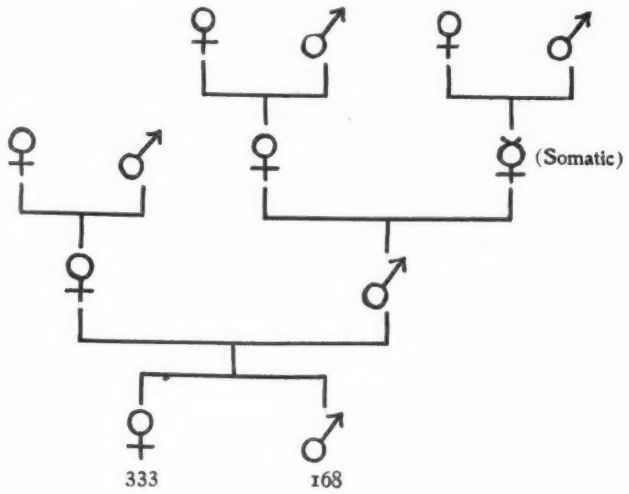

FIG. 15.—Model pedigree for case XIV

the view that the appearance of hermaphroditism in *C* and *D* was illusive, and that they were therefore only superficially like the genetic hermaphrodites *A* and *B*. These results fully justify my conclusion that the hermaphrodites of *Lychnis dioica* belong to two genotypes, one of which is the same as the normal male, the other different from it.

Discussion and conclusions

Although these data from the breeding of hermaphrodites of *Lychnis dioica* are presented in fourteen sections, each representing a somewhat different direction of attack upon the genetic problems involved, the results under the various sections are remarkably consistent. The hermaphrodites are clearly of two kinds. Those

included under cases I–XII produced male offspring like themselves when they were used as male parents (but not when used as female parents). These have been called "genetic hermaphrodites," to distinguish them from occasional genetic males which possess female organs as a purely somatic modification, and which I have therefore called "somatic hermaphrodites." These "somatic hermaphrodites" will be omitted from the discussion for the present.

Under cases II and III it is shown that genetic hermaphrodites, of whatever origin, when self-fertilized, yield dimorphic progenies consisting of females and hermaphrodites, thus confirming the conclusions derived from the F_1. This fact, together with the apparent relative ease with which males are made to exhibit the organs of both sexes, has been accepted as conclusive evidence that the hermaphrodites (and therefore also the males) are heterozygous with respect to sex, and the females homozygous (SHULL **26**). In this regard *Lychnis dioica* L. agrees with *Bryonia dioica* (CORRENS **6**); with many species of Coleoptera, Orthoptera, Hemiptera, Diptera, Odonata, and perhaps also with Myriapoda and Arachnida (MCCLUNG **19**, WILSON **38–42**, MORGAN **20, 21**, STEVENS **31–34**, etc.); and with the nematode worms, *Heterakis* (BOVERI **4**) and *Ascaris megalocephala* (BORING **3**). In man, GUYER (**16**) has demonstrated that there are two types of sperms, and while the relation of one or other of these types to the type of the egg is unknown, there can hardly be a doubt that here also the female is homozygous and the male heterozygous.[4]

Although these widely divergent groups of plants and animals agree in having homozygous females and heterozygous males, there may still be fundamental differences in the different groups, since there may be three different kinds of homozygotes, and correspondingly different kinds of heterozygotes. This question

[4] Heterozygous females have now been recognized in *Abraxas* (DONCASTER and RAYNOR **10**, and DONCASTER **8, 9**), sea urchins (BALTZER **1**), canaries (DURHAM and MARRYAT **11**), and in domestic fowl (BATESON **2**, SPILLMAN **28, 29**, GOODALE **12, 13**, HAGEDOORN **17**, PEARL and SURFACE **24, 25**, STURTEVANT **37**). GUYER (**14, 15**) reports two types of sperms in both the guinea fowl and the common fowl, but these observations are out of harmony with all the genetic studies in which sex-limited characters of the Gallinaceae have been involved. The considerable difficulties encountered in the cytological studies on these species suggest the advisability of a repetition of this work.

will be discussed later in connection with the nature of the hermaphrodites.

CORRENS (**6**, p. 17), with undoubted justification, maintained that the germ cells of monoecious, hermaphrodite, and dioecious species possess the tendency to develop into individuals having the distribution of sex organs characteristic of the particular genotype to which they belong; but when he likens the association of organs of both sexes in the same individual to the mosaic of red and white colors in striped flowers, and of pigmented and white spots in the coats of spotted animals, his justification becomes less obvious. Both striped flowers and spotted pelages are known from many investigations to be due to the presence or absence of a definite Mendelian gene, a so-called "spotting factor" or "pattern factor."

One of the chief aims in the arrangement of my cultures for 1910 was to test the possible existence of such a mosaic or "pattern factor," *H*, as a proximate cause of hermaphroditism in *Lychnis*, and the most striking result secured is the decisive manner in which such a possibility is denied. The hermaphrodite character is not only incapable of reaching expression in the female[5] (as might be expected, since the female is homozygous), but it is also as a rule not transmitted through the egg cell to the male offspring. The males in the progeny of any cross agree in their sexual type with the male parent of that cross, regardless of its antedecent history. All the assumptions and implications involved in the first section of table I, in which an independent gene *H* was postulated, may therefore be rejected.

[5] I refer here only to the normal functional hermaphroditism with which this paper deals, and not the pseudo-hermaphroditism which results when females of *Lychnis dioica* are attacked by the smut, *Ustilago violacea*, as reported by STRASBURGER (**35**). I was inclined (SHULL **26**) to consider STRASBURGER'S interpretation of the effect of *Ustilago* a mistake, as it appeared to me more probable that the infected plants were males whose heterozygous nature easily permitted the development of the female characters. STRASBURGER (**36**) has shown conclusively, however, by two series of facts, that his original observations and interpretation were correct. These facts are (*a*) that diseased plants are not always completely infected, in which case the uninfected branches of the pseudo-hermaphrodites have normal female flowers; and (*b*) that male plants may be infected also, but such infection does not in this case result in the development of the female organs.

In the second section of table I the hypothetical gene *H* for hermaphroditism is given limitations which make it fit all the empirical results of both the first and subsequent generations; but when the significance of the limitations is taken into account, it becomes evident that there is small advantage gained by the postulation of such a gene. Indeed the only advantage lies in the fact that in case the female is a positive homozygote, it keeps open the question whether or not there is a synaptic mate of *F* in the normal male; for a newly arisen hermaphrodite gene (*H*) might conceivably become a synaptic mate of *F*, even though the latter had had no synaptic mate in the normal male.

If the female is a neutral homozygote, that is, if the female gene *F* has a male gene *M* as its synaptic mate in the male, the hermaphrodite gene (if it exist at all) must be absolutely coupled with this male gene. In like manner, if the female is a negative homozygote *FFmm*, the *H* (if present) must be coupled with the male gene *M*. It is simpler, however, to assume that the hermaphrodite determiner is a modified form of the sex gene itself, than to suppose that it is a separate gene invariably coupled with the sex gene. This conception that hermaphroditism results from a mutative change in the sex gene, or in its homologue (?), the "Y-element," is made the basis of the last section of table I, but can apply only to those cases in which a male gene is present, or if not a male gene, then its homologue, a sexually indifferent gene which takes the place of *M* in the male; for if the hermaphrodite character is assumed to be due to a change in the female gene (*F*), as it must be if the latter has no "synaptic mate," the scheme will not work.

It appears to me impossible at the present time to determine whether the females of *Lychnis* are positive, neutral, or negative homozygotes. The facts seem to be equally well met by any of these assumptions; but the definite limitations of the hermaphrodite character to the males makes inapplicable the extreme form of the "presence and absence" hypothesis (that is, the hypothesis of unpaired genes) unless the female is a negative homozygote with reference to a male sex gene (*M*). While the possibility must be kept open that this is the relationship of the sexes in *Lychnis*,

it seems to me more probable that the female is a neutral homozygote (*FF*), the male having the formula *FM*, and the hermaphrodite the formula FM_H. The gradually increasing number of known instances of "spurious allelomorphism" proves that the pairing of unlike or unequal genes in the heterozygote is, if not the general condition, at least a not uncommon one.

The question whether the sex genes are paired or unpaired in the heterozygote, and if unpaired, whether the female is a positive or a negative homozygote, might be settled by simple observation, if it could be known that the chromosomes are the sex determiners, as a number of recent cytological studies clearly suggest. It is not at all certain, however, whether the unequal chromosome groups in the male-producing and female-producing germ cells are active *determiners* or simply passive *indicators* of other more fundamental differences. The latter possibility is strongly emphasized by MORGAN (**20**), who shows that the pole to which the accessory chromosome in *Phylloxera* is to proceed, is already determined before that chromosome has given any indication, by its own motion, to which pole it will go. This suggests that the poles of the dividing spermacyte may be sexually differentiated in advance by some other factor. If the chromosomes are not the sex-determiners, but only passive indicators, the fact that they are paired or unpaired, equal or unequal, has no decisive bearing upon the question whether the female is a positive, neutral, or negative homozygote, or whether the genes are paired or unpaired in the heterozygote, for it is quite as easy to assume that the movement of the accessory chromosome or "X-element" to the female pole takes place in response to a tension caused by the *absence* of a positive *male* sex-determiner at that pole, as that it is attracted by the *presence* of a positive *female* determiner. If the "X-element" should move into the vacancy caused by the absence of the sex-determiner, the presence of the added chromosome or group of chromosomes would become the evidence of the absence of the sex gene; in other words, the female possessing the added chromosome would be a negative homozygote. All this is highly speculative, and as there appears to be no way as yet to put the matter to experimental test, it seems futile to discuss further the question

whether the female of *Lychnis dioica* is a positive, neutral, or negative homozygote, or whether the synaptic mate of the female gene is qualitatively male or not. The matter has been considered at such length only because it is important that no unwarranted conclusions should be drawn from the configuration of the chromosomes in any given case.

There appears to be no very strong evidence at present that the chromosomes are the representatives or producers of particular Mendelian unit characters, though attempts have been made a number of times during the past decade to identify them as such. On the other hand, there is still no positive and complete demonstration that the chromosomes are *not* the determiners of the Mendelian characters, and until this demonstration is provided, the relation of the chromosomes to the unit characters must be kept open. Whether the chromosomes are responsible directly for sex may well remain likewise an open question for the present, especially in view of the fact that in many animals, and in the few plants which have been thus far investigated, no chromosome differences have been found to differentiate the sexes.

There can be no doubt of course that the sex characters are *associated* with chromosome differences in the considerable number of animals which have been found to present such differences, but, as we have just seen, the nature of this association is not clear. Where two types of sperms are found in the male, the one type corresponding in its chromosome complex with the single type presented by the eggs, the inference is fully justified that such males are heterozygous and the females homozygous in respect to sex, whether one or more chromosomes be the sex-determiner, or whether these chromosomes are merely symptomatic of other fundamental differences which are the true sex-determiners; and vice versa, when two types of eggs having different chromosome groups are found in the female, one of which agrees with the only type found in the sperms, the inference is fair that the female is heterozygous and the male homozygous in respect to sex. So consistent have been the results in those species in which both male and female germ cells have been investigated, that it has not seemed improper to assume that in any given species the one sex will have

uniform germ cells, and is to be considered homozygous, if the other sex is demonstrated to have two types of germ cells.[6]

No chromosome differences have been found in *Lychnis dioica* L. by STRASBURGER (**36**), who has studied a form of this species known in German taxonomic works as *Melandrium rubrum* Garcke. His careful investigation of germ cells and root tips showed 24 chromosomes to be the somatic number, one pair of these chromosomes being notably larger than the rest; thus resembling the accessory chromosomes or supposed sex chromosomes of the insects. However, in *Lychnis*, the two members of this pair are indistinguishable from each other in both the male and the female. The same results have been independently secured by Miss LUTZ during the past year, but have not yet been published. *Lychnis* appears to agree, therefore, with *Nezara*, *Oncopeltus*, etc. (WILSON **39, 40**), among the Hemiptera, as in these the two types of sperms, which doubtless exist, are not visibly differentiated. STRASBURGER (**36**) reports also that an investigation of *Bryonia dioica* has not revealed the two types of sperms that might *a priori* have been expected.

The hypothesis of unpaired determiners implies that a new Mendelian character originates by the formation of a new gene or the loss of an old one. My interpretation of hermaphroditism in *Lychnis dioica* as due to an alteration in a sex gene already in existence, which alteration does not in any way change the homology of the gene in question, calls for a fundamentally different method of origin of new characters from that involved in this extreme form of the "presence and absence" hypothesis. The new genotype which arises by mutation from the old one has in this case neither more nor fewer genes than had the genotype from which it originated.

The occurrence of male mutants among the offspring of my genetic hermaphrodites appears to me to have a bearing upon this question, as to the mode of origin of new characters. Among the offspring of genetic hermaphrodites tabulated in this paper, 11 male mutants appeared, and under case XII it is shown conclusively that these are true males, and do not again give hermaphrodite offspring, except probably in the extremely small proportion given

[6] As already noted, GUYER'S (**14, 15**) studies on spermatogenesis in the domestic fowl and in the guinea fowl appear at present to be exceptions.

by males not derived from a hermaphrodite family. These 11 males appeared in hermaphrodite families comprising a total of 5467 individuals, thus possibly indicating a somewhat greater coefficient of mutability than that reported for the production of hermaphrodites from normal males. It seems therefore that the modification of the gene *M* (or *f*) into a hermaphrodite gene *H*, and the reversal of this modification so that a normal male gene is again produced from a hermaphrodite gene, occurs with somewhat unequal facility, but the difference is not great enough to warrant the belief that mutation in the one direction is caused by the appearance of a new, independent organ, while its reversal is due to the disappearance of that organ. It seems to me more probable that these reversible mutations are due to reversible modifications of an element or organ continuously in existence, and not to the production of a new element or the dropping out of an old one.

The change from a male to a hermaphrodite condition and the reverse are processes both striking and sudden. Perhaps they are as fundamental mutations as those observed among the oenotheras. The interpretation given here of the process of mutation in the sex character of *Lychnis* seems to be available for other mutations as well. The sudden acquirement of new functions by a gene already in existence is different from the conception presented by DE VRIES in *Die Mutationstheorie*, to account for the origin of the *Oenothera* mutants, and is in accord with SPILLMAN'S "teleone hypothesis." SPILLMAN (**30**) is inclined to attribute the remarkable mutations in *Oenothera* to irregularities of mitosis, but in these sex mutants of *Lychnis*, abrupt genotypic modifications have taken place which can hardly be assigned to such irregular mitoses.

One puzzling feature of the inheritance of sex in *Lychnis* is the fact that self-fertilized hermaphrodites produce similar ratios of females and hermaphrodites as are produced when unrelated females are fertilized by sperms from hermaphrodites. Since it is obvious that the two types of offspring are due to the heterozygous character of the male, we are led to the conclusion that even though the hermaphrodite individual is heterozygous in respect to sex, its egg cells[7] are of a single type like those of the normal female

[7] Perhaps I should say "its *successful* egg cells."

and carry only the female tendency, while its sperm cells are of two types, one of which has the same sex character as the egg cells, the other bearing the hermaphrodite condition. In my preliminary paper, it was suggested that those eggs may fail to develop which lack the female gene *F*, or which possess the male gene *M;* or that in case the female is a negative homozygote, there might be an extrusion of the male gene during oogenesis. As there are no visible cytological differences between the females and the hermaphrodites, it may not be possible to decide these questions. The relatively small number of seeds in the hermaphrodites, as compared with the females, appears to be favorable to a selective elimination of male-bearing eggs. Another explanation seems possible. A segregation of the female and male genes may conceivably take place earlier than the time at which the germ cells are formed, though it must be admitted that there is little evidence at present that such early segregations regularly[8] take place in any plant or animal. Such a suggestion has been made by BATESON (**2**, p. 159), however, in the effort to account for certain interesting instances of coupling. If a segregation of female and hermaphrodite genes could be assumed to take place as early as the formation of a certain primordial cell from which the entire reproductive tissue of the ovary develops, so that the ovules are supplied only with the female genes, the observed uniformity of the egg cells would result. If segregation may take place thus before the spermacytes are developed, this might also offer an explanation of the exceedingly variable sex ratios which occur in *Lychnis*, for an unequally rapid development of tissues derived from female-bearing cells and male-bearing cells, from the moment of segregation until the spermacytes are produced, would give an unequal number of female-bearing and male-bearing sperms, and variability in this process would produce irregular ratios. I place no stress upon this hypothesis, however, and am inclined to look for an explanation of the observed phenomena in some sort of selective elimination.

There remains to be considered the relation of the somatic hermaphrodites to the problems of sex determination. The results under cases XIII and XIV show that the hermaphrodite

[8] They are known to take place occasionally in the production of bud sports.

character of these plants was purely superficial and did not affect the germ cells in any recognizable manner. The only bearing these plants have upon the question of sex determination, I think, is in the evidence they give that genetically normal males may be induced in some unknown way to exhibit female characters. When the male is interpreted as a Mendelian heterozygote in respect to the sex-producing gene, the occurrence of such a somatic modification has the appearance of a simple case of imperfect dominance, such as has been noted not infrequently in other Mendelian heterozygotes. However, the development of male organs (non-functional) in the supposedly homozygous female, when the latter is attacked by the smut (*Ustilago violacea*), gives support to the view held by STRASBURGER (**36**), that not only the heterozygous sex but both sexes contain in some degree the elements of the opposite sex or the capacity to react in the sexually opposite manner. This fact may perhaps indicate that sex is a more fundamental condition than might be inferred from the frequency with which it behaves as a Mendelian unit character. MORGAN (**23**) suggests a way in which the appearance of the organs or characters of one sex in individuals of the opposite sex may be explained in harmony with the Mendelian interpretation of sex determination. He assumes that there may be present, underlying the female sex gene, a male element with respect to which all individuals of both sexes are homozygous. This he indicates by introducing *m* into all of his sex formulae. In keeping with common usage among geneticists, he should have used *M*, since he intends to denote the *presence* of maleness.

While recognizing the aptness of this suggestion in removing some of the difficulties in the way of a general application of the Mendelian explanation of sex, I am inclined to the view that the Mendelian nature of sex is of secondary rather than of primary consequence. May not maleness and femaleness be thought of as alternative states, which can be crudely analogized with the acidity and alkalinity of chemical solutions? Just as solutions may be made acid or alkaline in different ways, either by qualitative or by quantitative additions, subtractions, or substitutions, or by a combination of qualitative and quantitative changes, it

is conceivable that the alternative sexual types may be determined in different cases by very different methods, some qualitative, some quantitative, and others both qualitative and quantitative. In some species the sexes appear to represent a much more strongly polarized (?) condition than in other species, and a transition from the characters of the one sex to those of the other is attained only with the greatest rarity, if at all; while in other species the sex conditions may be so nearly balanced or neutral that individuals are not so absolutely determined in their sex relations by their genotypic nature, thus resulting in ever-sporting varieties in respect to sex, such as CORRENS (**7**) has found in *Plantago lanceolata*.

With such a conception of sex, it also appears probable that sex may be influenced sometimes by external factors as well as by internal ones, and in this case the preponderance of one sex over the other, which has been observed in many animals and plants, need not be attributed alone to a selective disorganization of germ cells, a selective fertilization, or a selective death rate, but might conceivably be controlled to a certain extent by environmental conditions acting at some particular "sensitive period" in the ontogeny of the organism in question. However this may be, there is little or no evidence at present that such environmental influences on sex can be more than relatively slight in the case of dioecious plants and animals. In such organisms recent genetic and cytological studies prove conclusively that sex is generally determined by the genotypic nature of the individual.

Summary

The hermaphrodites of *Lychnis dioica* are modified males. They are of two kinds, which are here distinguished as "genetic" and "somatic" hermaphrodites.

When the genetic hermaphrodites are used as pollen parents, either when self-fertilized or in crosses with females, their progenies consist of females and hermaphrodites. When they are used as pistil parents, and fertilized by normal males, they produce females and normal males.

Somatic hermaphrodites may be externally indistinguishable

from the genetic hermaphrodites, but when used as pollen parents they produce no hermaphrodite offspring, but only females and normal males.

The fact that males can be modified so as to produce functional organs of both sexes, indicates that they are sex heterozygotes, and the production of both females and hermaphrodites by self-fertilized hermaphrodites strongly supports the same interpretation.

The hermaphrodite character can neither find expression in the females, nor can it be transmitted by their eggs to the male offspring. Consequently it is not determined by an independent gene, H, but by a modification of the male sex gene, M, or of the "synaptic mate" of the female gene, F.

If the males and hermaphrodites are heterozygous, it follows that the females are homozygous; but this does not offer an ultimate solution to the relationship between females and males, since there may be several different kinds of homozygotes and heterozygotes. As applied to the relation of the sexes, these may be indicated by the following formulae: (*a*) The female may be a "positive" homozygote; then FF=♀, Ff=♂, Ff_H or FH=☿. (*b*) If the female is a "negative" homozygote, $FFmm$=♀, $FFMm$=♂, FFM_Hm=☿. (*c*) When the female is a "neutral" homozygote, FF=♀, FM=♂, FM_H=☿. In each of these formulae the subscript H is intended to represent a modification of the gene to whose symbol it is appended, such that the male is changed to a hermaphrodite. Which of these formulae correctly represents the condition in *Lychnis* can not be determined, but the modified gene which results in hermaphroditism is allelomorphic to F unless the female is a negative homozygote.

Among the offspring of genetic hermaphrodites were a small number of male mutants (11 in 5467), which on breeding proved to be normal males. The occurrence of these male mutants indicates that the modification to the hermaphrodite condition, and back again to the male condition, occurs with but slightly unequal facility, and this circumstance is believed to favor the view that mutation in this case depends upon reversible modifications of some permanent element or organ, rather than upon the origination of a new unit, and its disappearance. This interpretation

bears both upon the nature of mutation and upon the real significance of the "presence and absence" hypothesis.

STRASBURGER has shown that females of *Lychnis dioica* attacked by *Ustilago violacea* become pseudo-hermaphrodites through the production of stamens, which however are non-functional, owing to the fact that the smut produces its spores in the anthers. This seems to justify his conclusion that each sex possesses some of the potentialities of the opposite sex.

The view is expressed that the sexes represent alternative states which in different species may be attained in various ways, through either quantitative or qualitative changes, additions, subtractions, substitutions, or transformations, and that in some instances the action of environment may prove effective in determining which of these states shall find expression. Nearly all the recent investigations indicate, however, that sex is at least predominantly dependent upon the genotypic nature of the individual.

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REPRODUCTION BY LAYERING AMONG CONIFERS

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WILLIAM S. COOPER

(WITH ONE FIGURE)

Many types of plants multiply more or less by layering, or may be made to do so by artificial means. The fact seems not to be well known that various conifers, particularly members of the genera *Picea* and *Abies*, possess this power and multiply by it to some extent. Having by accident discovered a case of layering in the balsam fir (*Abies balsamea* [L.] Mill.) during the course of ecological work on Isle Royale, Lake Superior, I found that the habit was a factor of considerable importance in the dynamics of the forest. Investigation into the literature of the subject brought to light a few scattered references to layering of coniferous trees, which are noted below. It is not probable that the list is exhaustive.

I. Literature

The earliest description that was found was contained in LOUDON'S *Arboretum et Fruticetum Britannicum* (**8**), vol. IV, pp. 2297–2298. The author quotes Mr. JAMES M'NAB in *The Gardener's Magazine* as follows:

> From the pendent habit of the lower branches of the spruce (*Picea excelsa* Link) some curious anomalies are occasionally found in its habit of growth. The shoots next the ground, when they have attained a considerable length, naturally rest on the soil at their extremities; and the soil being kept moist by the shade of the branches, these often root into it; and the points of their shoots taking a vertical direction, a series of new trees are formed in a circle round the old tree.

A particular specimen, growing in Scotland, is described thus:

> Many natural layers from the trunk and from the primary substems have taken root, so as to form a double series of young trees in two concentric circles round the parent trunk.

A little farther on is the following:

> That portion of the branch which is between the trunk of the original tree and the part where it roots into the ground, and which is sometimes several feet in length, rarely increases in diameter after its extremity has rooted. . . . .

The branches proceeding from the primary substems have also branches, equally healthy with themselves, proceeding from them, and with every appearance of their producing others. . . . . The primary substems, which constitute the inner concentric circle of young trees, vary from 8 feet to 25 feet in height; and the secondary substems, which form the trees of the outer circle, are from 4 feet to 10 feet high. There are upward of thirty rooted stems surrounding the mother tree, and 30 feet is the greatest diameter of the space covered by stoloniferous branches; though in one case a secondary layer has reached as far as 18 feet from the main trunk.

LOUDON also mentions cases of abundant layering in *Abies nigra* (*Picea mariana* [Mill.] BSP.).

KUNZE (**7**) also refers to M'NAB'S observations and concludes from these and other cases that "Coniferae, especially the Abietineae, possess widely extended power of root formation and are able to send out rooting shoots."

KIHLMAN (**6**) notes that *Picea excelsa* growing at the arctic tree line in Lapland spreads extensively by layering. He describes the occurrence of the habit as follows. The lowest branches often have roots, and from their tips new erect shoots develop, which become treelike in form and come to lead independent lives; from this results a complex of shoots and small trees of various ages, which is very sharply bounded, and which often arises from a single parent. Such a group, 4 meters in diameter, included 42 stems more than 4 cm. thick, besides numerous smaller ones. The age of such a centrifugally spreading group of spruces may almost be unlimited. He distinguishes two habit varieties of *Picea excelsa*. One possesses a tall cylindrical crown, often extending to the ground, the lower branches seldom rooting, and the life of the individual thus ending with the death of the main trunk. The other variety, characteristic of the region of the northern limit of the spruce, is low and scrubby, and layers abundantly as described above.

CHRIST (**2**) refers to layering in *Picea excelsa* as of rare occurrence, and names such forms *Picea excelsa forma stolonifera*.

GOEBEL (**5**) mentions cases of layering in *Picea excelsa*, *P. nigra*, and *Abies sibirica*.

SCHRÖTER (**11**) describes and illustrates something very similar in the case of *Pinus montana* in the timberline belt of the Alps.

He speaks of "horizontal snakelike branches crawling over the ground, ascending or erect at the ends," but does not state, nor do his figures show, that these branches take root.

According to MAYR (**9**) all deciduous trees and conifers are able to produce roots when branches or weak stems are bent down and placed in contact with the ground for a time. He mentions the following genera as among those that have been observed to reproduce by layering: *Abies*, *Picea*, *Pinus*, *Larix*, *Pseudotsuga*, *Chamaecyparis*, *Cryptomeria*.

MIGULA (**10**) briefly notes the habit, and gives an illustration of a spruce (*Picea excelsa*) surrounded by a circle of young trees developed from layered branches.

VOGTHERR (**13**) speaks of the habit as occurring frequently, though often overlooked, and states that it is commonest in moist habitats in northern latitudes and in mountain regions.

Reproduction by layering among conifers has been reported in America, so far as I have been able to discover, in two species only, both of the genus *Abies*.

SUDWORTH (**12**) in discussing the reproduction of the alpine fir (*Abies lasiocarpa* [Hook.] Nuttall) says (p. 111): "Occasionally at high elevations branches lying on ground take root (layer), from which, however, reproduction is probably rare."

In *Silvical Leaflet* (**4**) of the Forest Service, devoted to *Abies lasiocarpa*, is the following paragraph:

> Alpine fir frequently exhibits a tendency to reproduce by layering. The lower branches, which are procumbent, become covered with earth, roots are produced, and the branches increase in size and assume an upward curve. It is doubtful, however, if the tree ever actually reproduces itself in this manner. The tendency becomes more apparent with increasing altitude, the main trunk becoming shorter, while the layered branches form a saucer-like whorl at its base.

CLEMENTS (**3**), speaking of the same species in the Colorado mountains, states that "all the young firs examined had started by layering from the lower branches of parent trees."

Concerning the eastern balsam fir (*Abies balsamea* [L.] Mill.) I have found but one notice of the habit. CHITTENDEN (**1**) in discussing the timberline trees of the White Mountains says:

Balsam, at such elevations, rarely matures its seed, reproduction being dependent on seed blown up from below and on the layering of the trees themselves. Branches so layered are often found growing as independent trees, the connecting branch having decayed. The rooting always proceeds from dormant buds. Prostrate balsam occurs at an altitude of 5500 feet on the Presidential Range, where it reproduces almost entirely by layering. At an elevation of 4900 feet cones are borne sparingly, but even here reproduction by layering exists.

II. Layering as observed on Isle Royale, Lake Superior

Upon Isle Royale the layering habit manifests itself as follows. In the forest one frequently comes upon small groups of young balsams, often of about half a dozen individuals of various sizes. These upon superficial inspection would easily pass for a cluster of seedlings, but if the group be carefully dug up, all the young trees will be found to be connected with each other a little below the surface of the ground. The way in which the layering comes about was found to be as follows. The lower branches of the balsam droop more or less, and the middle portion of such a branch frequently becomes covered with moss, litter, and humus. If the point of origin of the branch is very close to the ground, the connection soon becomes entirely concealed; this seems to be the case more often than otherwise. The covered portion now produces roots abundantly, and the tip becomes erect, loses its dorsiventral character, takes on radial symmetry, and is to all appearances a perfect miniature tree.

Layering may take place at any stage in the life of the tree. Sometimes the layered branch may be only a few years younger than the parent and not very perceptibly smaller, showing that it must have developed from one of the very earliest branches. Mere seedlings were sometimes seen with layered branches about as large as the parent. The daughter trees often produce a second generation, and it is in this way that the groups of apparently independent saplings come into existence. On the other hand, cases were found where a mature tree was layering through branches that had their points of origin a number of decimeters above the ground. Several of the lower branches of a mature tree may layer, producing a circle of young trees around the parent, and numerous

cases were found in which the layered branches themselves had given rise to secondary groups, the connection with the original tree being still maintained.

There is abundant evidence that in many cases the layered branches become independent trees by the decay of the connecting portions. In fig. 1 it may be seen that the layered branch near its point of origin is extremely slender, while in the region where the roots have developed and in the subaerial portion it is thick. The transition from thin to thick is frequently very abrupt. This points toward the conclusion that the young tree is deriving by far the greater amount of its sustenance from its own root system, and that if the connection should be broken it would be entirely able to care for itself. The underground portion was often so weak that in spite of the greatest care it was severed in the process of uprooting. In many cases also the decumbent bases of independent young balsams indicate that they once had a horizontal connection with some neighboring tree (see *a* in fig. 1).

Some examples will make clear the various forms which the habit of layering takes.

1. A very typical case is seen in fig. 1. The oldest stem shown in the photograph is at *1* (all but the base has been removed for the sake of clearness). That this is itself a layered branch of a still older tree is indicated by the long rhizome-like structure (*a*) extending horizontally toward the left. The character of the well formed young tree *2* as a layered branch of *1* is evident. Branch *2* is one meter high. Branch *3* is connected with *2* by way of *c*, and has itself given rise to *4;* the latter finally has produced *5*. There are thus represented five generations of upright stems produced by repeated branching and layering. Each except the youngest possesses a well developed root system of its own, and in every case except the last the horizontal connecting stem behind the region of vigorous rooting has remained practically without further development. The constriction where *b* joins *1* is especially evident. Branch *5* receives all its nourishment from *4*, and the latter probably still derives much from *3*.

2. A balsam 2 meters high, which had died very recently at the age of 46 years, itself apparently a layered branch, had given rise

through a lower branch to a young tree 7.5 dm. high, 24 years old, 2.5 dm. distant from the parent. This daughter tree was found to have produced four smaller ones, 1.5–6 dm. in height, with ages ranging from 16 to 22 years.

3. That the habit may show itself even in large and mature individuals is proved by the following case. This tree, a balsam

FIG. 1.—An example of layering as it commonly occurs on Isle Royale, Lake Superior; *Abies balsamea*.

1.5 dm. in diameter and 85 years old, had given rise to a daughter tree through a layered branch which started 7.5 dm. above the ground. The outer portion of this branch was soil covered and had well developed roots. At a distance of one meter from the parent it became a symmetrical tree 1.3 m. high. The same large branch had also produced two smaller trees by the layering of secondary branches.

4. A balsam growing in a large rock crevice at the forest edge on an exposed shore had several layered branches, erect at tip, through the soil at the general level of the ground. Several similar branches, at about the same elevation but in line with the crevice, descended into it somewhat, but their ends were erect, radially symmetrical, and perfectly treelike. Since the crevice was a foot wide and contained no soil, no roots were formed in this case, and these branches remained entirely dependent upon the tree.

Aside from the balsam, layering was less frequently observed in every one of the coniferous trees that occur upon Isle Royale. It was fairly common in the case of the black spruce, perhaps being favored by the pronounced droop of the lower branches of that species. The black spruce occurs sparingly in the upland forest, and in this habitat the layered branches were identical in behavior with those of the balsam. Black spruces and tamaracks growing in bogs were found to layer abundantly through the rapidly growing sphagnum. Specimens of white spruce were found upon nearly bare rocks, whose lowest branches, covered with a thin mantle of humus, had developed the layering habit to such an extent that the parent had become entirely surrounded by a group of daughter trees. Similar groups were seen in the case of arbor vitae growing in a river swamp.

III. Conclusions from data presented

From the material here presented we gather that the habit of natural layering among coniferous trees is common and widely distributed, though its importance appears to have been generally overlooked, at least in this country; that it is particularly characteristic of the closely related genera *Picea* and *Abies*, but is found in many other genera, among which are *Larix*, *Thuja*, *Pinus*, *Pseudotsuga*, *Chamaecyparis*, and *Cryptomeria;* that it is most prominent in northern and mountain regions, and that it occurs more frequently and attains more striking development with increasing latitude and altitude; that its best development is found at the extreme limit of the forest—the arctic tree line and the mountain timberline.

The general region of its occurrence is practically that of conifer

dominance; its increased development in high latitudes and altitudes is not so easily explained. VOGTHERR (13) correlates the layering tendency with a moist habitat, made possible by the low evaporation rate in northern and mountain forests, and it is doubtless true that moisture and absence of light are the factors that stimulate the buried portions of the branch to root production. But cases were noted (see example 4 above, and also SCHRÖTER 11), in which, although the end of the branch became erect and treelike, no portion was buried, and therefore no roots were formed. In other cases trees with layered branches were found growing in xerophytic situations upon the exposed rocky shores of Lake Superior. Timberline conditions, too, more often than not, are xerophytic in the extreme. The connection with a moist habitat thus seems not to be an essential one. In explanation of the striking cases of layering reported from the tree line in various regions (circles and double circles of daughter trees surrounding the parent), it may be noted that in such localities the forest is open, and the trees therefore, on account of abundance of light, are clothed with living branches to the ground. Moreover, they are as a rule short, bushy, and branchy, and the low crown tends to spread horizontally rather than to increase in height. Just such conditions as are found here (numerous healthy branches close to the ground) are those which would apparently most favor the appearance of the layering habit. In the endeavor to solve the problem, however, the meagerness of the data should be borne in mind. It may be that more extended and careful observation would prove that the habit is as common at low latitudes and altitudes as at high. Possibly the greater number of reports from arctic and alpine regions is due to the fact that the phenomenon is most easily observed there, or that individual cases of more striking appearance have been found. On Isle Royale, though the habit was exceedingly common, no such remarkable examples were discovered as those reported by LOUDON and KIHLMAN.

IV. Ecological importance of layering

The habit of layering, in regions where it occurs, must be included as an important factor in any investigation of forest

dynamics. For example, in the climax forest of Isle Royale there is an appearance of thick reproduction, with a great preponderance of balsam in the young growth. Upon superficial examination one would conclude that reproduction by seed is taking place at a tremendous rate. Careful investigation reveals that a large proportion of the apparent seedlings are in reality merely layered branches, some of them having originated from mature trees, and many others being groups of connected shoots which have started from a single true seedling. The same situation was found by CLEMENTS (3) in Colorado. It is evident that the effectiveness of this method of reproduction will have an important bearing upon the course of the succession in the forest. The habit is of special importance in the region of timberline, where, according to authors quoted above, it is sometimes almost the only method of reproduction.

V. Physiological bearing

There are also physiological problems involved in the phenomena of layering in this group of plants, which cannot at present be satisfactorily settled. These problems relate to the theories of orthotropism and plagiotropism and their mutual relations. The whole subject is at the theoretical stage, without adequate evidence in support of any of the various hypotheses. In the process of layering, the rooting (when it occurs) is simple enough as a response to moisture and absence of light. The change from dorsiventral to radial symmetry is to be expected as a result of the tip becoming erect, being an adjustment to changed light relations. The change in direction of growth from horizontal to erect is the part that is difficult to explain. It is bound up with the agencies which cause lateral shoots, ordinarily plagiotropic, to become orthotropic when the terminal shoot is removed or damaged. In the process of layering, it should be noted, this change takes place without antecedent removal of the main shoot. The case is thus somewhat different, but the same factors doubtless govern it. In the present state of knowledge relating to orthotropism, plagiotropism, and correlation, it will be useless to continue the discussion at length. One point however seems to be important enough in its bearing upon the

physiological side of the question to justify a few words in conclusion. GOEBEL (**5**, chapter iii), to explain the replacement of the terminal by a lateral shoot, offers the theory that the change in direction of growth of the lateral comes about because of changed conditions of nourishment. He thinks that the main transpiration current, which ordinarily goes to the terminal shoot where growth is most vigorous, is deflected when the terminal shoot is removed, and passes into the uppermost lateral. The great increase in nutrition acts as a stimulus, causing the lateral shoot to become erect. He describes several cases of layering among conifers, and attributes the change in direction of growth of the layered branch to the same factor. In this case the increased amount of food materials which acts as the stimulus is furnished through the agency of the newly formed root system. This theory would fit most of the cases of layering which have been described, but in one example which came under my observation on Isle Royale (no. 4 above) the change of direction of growth took place with absolutely no root formation. The same is probably true of those described by SCHRÖTER (**11**). Here are cases, therefore, where GOEBEL'S explanation certainly does not hold, and so far as this bit of evidence goes, it throws doubt upon his theory as a whole.

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THE ENDOSPERM OF ANGIOSPERMS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY **150**

JOHN M. COULTER

In a recent analysis of all the available testimony in reference to the morphological nature of the endosperm of angiosperms, it seemed clear that certain conclusions might be reached, and the purpose of the present paper is to state them.

It has been assumed that the endosperm must be either gametophytic tissue or sporophytic tissue, and the arguments for each view are familiar. The perplexity has arisen chiefly from the feeling that gametophyte and sporophyte must be subject to rigid definition. When definitions become rigid, ideas become rigid also, and nature is always playing havoc with rigidity. If gametophytes and sporophytes are defined as x and $2x$ structures, respectively, straightway x sporophytes and $2x$ gametophytes are discovered. If sporophytes are defined as structures produced by fertilized eggs, the definition is contradicted by numerous sporophytes that are not the product of fertilization. In this way, every criterion suggested has found its contradiction. It is becoming evident that definitions must be elastic and not rigid, and that general situations rather than definite categories must determine conclusions. We have moved so far beyond the rigid categories of the days of metamorphosis, that it is surprising to find an equal rigidity in the days of alternation of generations.

Without citing an extensive and familiar literature, attention may be called to the various claims that have been made as to the morphological nature of the endosperm of angiosperms.

Ever since the comparative morphology of the vascular groups was uncovered by HOFMEISTER, belief has been general that the endosperm of angiosperms is gametophytic tissue which develops after fertilization. It was easy, even in the days of HOFMEISTER, and much more so now, to obtain from gymnosperms what seems to be abundant confirmation of this claim. Throughout that group there is a distinct tendency to differentiate eggs earlier and earlier

in the ontogeny of the gametophyte. When this differentiation occurs along with the first appearance of tissue after the free nuclear stage (as in *Torreya*), it is clear that the great bulk of endosperm tissue is developed after fertilization. When the differentiation occurs during the free nuclear stage (as in *Gnetum*), it is clear that all the endosperm tissue is developed after fertilization. It was very easy, therefore, to see in the endosperm of angiosperms only belated gametophytic tissue.

When the relation of the polar fusion to endosperm formation began to be appreciated, LE MONNIER (1887) suggested that this fusion is a sexual act, and that therefore the endosperm is sporophytic. This would mean that the embryo and endosperm are twin sporophytes, the latter for some reason not developing the organization of an embryo. This explanation of the polar fusion does not seem to have met with much approval. It is important to note, however, that lack of approval was probably due to the fact that there had developed already a considerable knowledge of the great freedom of nuclear fusions within the embryo sac and within the endosperm. Clearly all such fusions could not be sexual.

With the discovery of "double fertilization," the endosperm problem became conspicuous. One of the nuclei that enters into the triple fusion is plainly a male nucleus; one of the polar nuclei is sister to the egg nucleus, and this was taken to indicate its sexual character; the other polar nucleus has been regarded as vegetative in character. The fusion of an undoubted male cell and an assumed egg was regarded as an act of fertilization, and the product of such a fusion must be a sporophyte. This conclusion as to the nature of the endosperm is inevitable if the triple fusion is to be regarded as involving a sexual fusion.

If the endosperm is a sporophyte, it must be explained why it does not become organized as an embryo, but remains as formless tissue. Miss SARGANT (1900) offered a very ingenious explanation, effectively supported by what seemed to be confirmatory evidence. According to this explanation, the endosperm remains a formless mass of tissue (a "monster") because a vegetative nucleus enters into the fusion and interferes with the legitimate result. This view is attractive, but hardly explains the increasing number of

cases in which the so-called vegetative nucleus does not enter into the fusion, and still the product is only endosperm.

STRASBURGER analyzed the situation, and held to the original interpretation of the endosperm as gametophytic tissue, on the plea that there are two aspects of fertilization, one being fertilization as a stimulus to growth, the other being fertilization as a transmission of hereditary characters. These two aspects he designated respectively vegetative fertilization and generative fertilization. He saw in the result of the triple fusion only a stimulus to growth, resulting merely in tissue, and not a transmission of hereditary characters, which would express itself in an organization. Unfortunately for this view, all the phenomena of xenia are against it, for in such cases it is quite evident that characters of the pollen parent are transmitted to the endosperm by the male nucleus that enters into the triple fusion, but of course there is no sporophytic organization.

Furthermore, the cytological test for the two generations breaks down in this case, as it had in cases of apogamy and apospory, for the endosperm number of chromosomes, in case triple fusion has occurred, is neither x nor $2x$, but at least $3x$. To speak of $3x$ gametophytic tissue is to use some other test than the number of chromosomes. It must not be understood that this in any way affects the general contrast between gametophytes and sporophytes on the basis of chromosome numbers. A generation that follows a reduction division is of necessity an x generation; and one that follows fertilization is a $2x$ generation. But when the reduction division or fertilization does not occur, and still another generation follows, the chromosomes of that generation must become unusual in number, following an unusual situation.

It will be helpful to consider the cases of endosperm formation that do not involve triple fusion. This will enable us to recognize the fact that the origin of endosperm is not necessarily related to the triple fusion, and that we have in endosperm a constant product arising from variable antecedents. It is simple to put such cases into two categories: (1) multiple fusions, and (2) no triple fusion.

(1) The well-known case of *Peperomia* may represent the category of multiple fusions. In the fusion of 8–14 nuclei to form

the "primary endosperm nucleus," we observe an act too miscellaneous to represent anything so definite as fertilization. Moreover, we obtain positive evidence that in the embryo sac there is some condition that favors nuclear fusions, quite apart from what may be called sex attraction.

(2) Cases of no triple fusion, followed by endosperm formation, are numerous. In some instances, there is not even polar fusion, each polar nucleus initiating endosperm formation independently. In other cases, the male nucleus may fuse with either of the polar nuclei, the other nucleus remaining out of the combination, but the result is always the same. When the male nucleus pairs only with the micropylar polar nucleus, one might expect an embryo, if the latter nucleus is really an egg, but endosperm is the result. The increasing number of known angiosperms which are habitually parthenogenetic furnish cases of endosperm formation in the absence of the male nucleus. Of course in such cases the endosperm may be claimed to be parthenogenetic also.

The cases of so-called parthenogenesis among angiosperms illustrate a wider variation in the antecedents of endosperm formation than the mere absence of the male nucleus would seem to indicate. STRASBURGER has called attention to the fact that in the cytologically investigated cases of parthenogenesis there has been no reduction division, and that therefore the parthenogenetic egg is a $2x$ egg, just what it is after normal fertilization. If the failure of reduction results in a $2x$ egg, it must result also in $2x$ synergids, antipodals, and polars; in other words, the gametophyte has throughout the sporophyte number of chromosomes. And still, endosperm formation proceeds as before, when one would be justified in expecting embryo formation by sporophytic budding, a phenomenon very common in the tissues adjacent to the embryo sac. No one questions that the embryo is a sporophyte, whether it is a result of the act of fertilization or not, for it is recognized by its organization. It is pertinent to ask, therefore, why there should be any hesitation in recognizing the endosperm as gametophytic from its lack of organization, no matter how it originates. It is obvious that the constancy of endosperm lies in its structure and not in its origin.

From the facts in hand, the following statements seem to be justified:

(1) Endosperm formation is not dependent upon the presence of a male nucleus.

(2) Endosperm formation is not even dependent upon polar fusion.

(3) Therefore, both of these fusions may be regarded as *supplementary* rather than *determinative*.

(4) Endosperm formation does not even depend upon having been preceded by a reduction division.

(5) The fusions associated with endosperm formation do not represent a definite process, but are miscellaneous in number and order.

(6) The product of such fusions as do occur is merely an undifferentiated tissue, which practically continues the tissue of the gametophyte; that is, it is simply *growth* and not *organization*.

Conclusions

It seems evident that the egg has an organization peculiar to itself. A male cell may fuse with any other cell in the sac, and the result is only endosperm; but occasionally such a fusion (as with a synergid or a polar) results in an embryo. This implies that, for some reason, these ordinarily sterile cells have achieved the organization of eggs. It is this possibility that makes them *potential* eggs; but in the ordinary embryo sac of angiosperms there is only one *actual* egg, which means only one cell capable of being fertilized in any real sense, and therefore capable of producing an embryo.

Conditions in the embryo sac favor fusions of any free nuclei, in any number and of any origin. A male nucleus, perhaps, is more apt to enter into fusions than any other kind.

A male nucleus entering into a fusion may or may not express itself as a carrier of hereditary characters. If it does express itself in this way, it is like injecting certain gamete tendencies into a vegetative fusion; therefore, it is more probable that the male nucleus modifies somewhat the normal product than that the antipodal polar (a vegetative nucleus) modifies a normal product. In

other words, the vegetative fusion is more apt to represent the normal situation than a sexual fusion.

There is no necessary phylogeny of such a performance. It is more a physiological problem to discover the conditions in the embryo sac of angiosperms that favor miscellaneous nuclear fusions.

The final conclusion seems to be that free nuclei within the embryo sac, containing a variable number of chromosomes and reacting to one another in various ways, are in a condition to continue division, and this division is usually carried forward to tissue formation. The whole history of the megaspore and its products justifies us in regarding this tissue, however formed, as gametophytic.

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NOTE.—Since this paper was in type, there has appeared a paper by CAMPBELL on the embryo sac of *Pandanus*,[1] which supplies another illustration of the indefiniteness of the nuclear fusions within the sac. In this case there is an extraordinary development of antipodal tissue before fertilization, and a varying number of free antipodal nuclei fuse with the micropylar polar to form the large primary endosperm nucleus. In some cases two primary endosperm nuclei may be formed by these multiple fusions, and it would seem to make no difference in the result whether the "second male nucleus" fuses with one of them or with neither of them. In either event, it is obviously a vegetative fusion.

[1] Ann. Botany **25**:773–789. *pls. 59, 60. figs. 2.* 1911.

SOME PROBLEMS IN CECIDOLOGY

MEL T. COOK

It is very doubtful if any phase of biology has been neglected more than that very conspicuous and extremely puzzling branch known as cecidology. This subject in its broadest sense includes all forms of abnormal plant growth regardless of cause. It must include, therefore, not only the hypertrophies, but also the witches brooms. It must include the abnormal growths caused by flowering plants, fungi, bacteria, insects, nematodes, and chemical and mechanical injuries. It must also include that great number of abnormal growths from unexplained causes which are included under the general term of teratology. Unfortunately, many of the botanists have interpreted the subject to include only those cecidia which are the result of insect injuries, and have attempted to relegate the entire subject to the entomologists, although they have not hesitated to study the cecidia caused by nematodes and bacteria, which might just as reasonably be forced upon the zoologist and bacteriologist.

The fact that the mycologists have usually been interested in the fungi and not in the host plant, explains why so much interesting material has been thrown aside with the single comment, "bugs." But with the development of plant pathology, a branch of botany which is necessarily interested in the pathological condition of the host, there is no longer any excuse for not giving a reasonable consideration to all phases of cecidology.

It is the purpose of this paper to call attention to some of the problems involved in cecidology, and to their bearing on other phases of biology, more especially botany. Cecidology is as old as the science of biology, and cecidia are referred to in some of the earliest biological literature. That cecidia were the subject of speculation, if not of study, is evidenced in the writings of REDI,[1] who, like other vitalists of his period, believed plants were endowed with souls and that the soul of the plant controlled the formation

[1] REDI was born in 1626.

of both the egg (i.e., the gall) and the insect which emerged from it, and determined their specific characters. As in all other biological subjects, the first real scientific work was taxonomic in character, and in 1686 MALPIGHI, who was a physician to Innocent XII and professor of medicine in Bologna and later in Messina, published his *De Gallis*, in which he gave quite accurate descriptions of the known galls of Italy and Sicily. Following this work, which may be looked upon as the starting point for cecidology, LINNAEUS and many other later writers gave more or less attention to this subject, which has attracted so much attention in Europe during recent years. In America, the pioneers in this subject were Baron C. R. OSTEN-SACKEN, BASSETT, WALSH, RILEY, FITCH, SHIMER, and HARRIS, all of whom were entomologists.

Although the entomologists have done more work in cecidology in both Europe and America than the botanists, their work has been no broader. The entomologists have studied the insects and described the cecidia which were attributed to them, and in the case of the injurious species have devised means for their control. The botanists have done the same work for fungi which cause cecidia, and have also invaded the fields of the bacteriologist and zoologist and studied not only the cecidia produced by bacteria and nematodes, but have even studied the organisms.

Taxonomy seems to be the forerunner of all lines of biological work, and this has been true of cecidology, but we have now reached a point from which we can extend our studies into other phases of the subject. We can now study the subject with reference to other phases of biology, in fact other phases of biology are encroaching upon the subject of cecidology. With this new development, the entomologist, the mycologist, and others will continue to find ample fields for the study of taxonomy. The entomologist will also have those almost untouched fields of life history and of alternation of generations which came so near to demonstration by our fellow-countrymen, H. F. BASSETT, and which was afterward demonstrated by HERMAN ADLER.

The various groups of botanists will find especially rich and almost untouched fields in many directions. The anatomical and histological characters and the development of cecidia have

been the subject of extensive studies in Europe, but have received very little attention in America. These studies when properly carried out and correlated with the work of the taxonomists will in turn open broad and unexplained fields in evolution. The pathology of the plants which are suffering from the attacks of these many cecidia-producing organisms cannot be overlooked by the plant pathologists, who have no more right to refer insect cecidia to the entomologist than the surgeon has to send the patient suffering from a gun-shot wound to the gunsmith. Both the economic entomologist and the plant pathologist will find enough problems to keep them busy for many years to come. It is doubtful if the entomologist has said the last word on the *Phylloxera vastatrix*, *Schizoneura lanigera*, *Eriophyes pyri*, and many other cecidia-producing insects which attack economic plants; and it is undoubtedly true that the plant pathologist has scarcely touched many of the economic problems involving cecidia-producing fungi and bacteria. The cytologist will also find a field for his labor.

However, the most difficult and probably the most fruitful field is open to the plant physiologist; the character of the stimuli which excite malformation is a question well worth the attention of any group of scientists, and one which if answered may be very far reaching in its influence. The botanists have doped the plant with many chemicals, with some of which it may never come in contact in a state of nature; they have subjected it to the various kinds and degrees of gases, light, moisture, and temperature; treated it with electricity; prodded it with everything imaginable from a most delicate needle to a crowbar; and otherwise subjected it to various normal and abnormal conditions, but have made little or no effort to determine the character of the stimuli which cause the formation of cecidia. DARWIN and all his predecessors believed that the cecidia are directly or indirectly the result of a chemical secreted by the mother insect at time of oviposition; MALPIGHI believed that the chemical causes a fermentation of the juices; REAUMUR[2] held the same view, but also believed that the thermal effect of the egg and the character of the wound, which varies with the different species of the insect, are important factors. Sir

[2] Mémoires pour séries à l'histoire des insectes. Mémoire XII. Vol. III. 1738.

JAMES PAGET, as late as 1880, said that "the most reasonable, if not the only reasonable theory, is that each insect infects or inoculates the leaf or other structure of the chosen plant with a poison peculiar to itself." Unfortunately, this view is still held by most of our biologists, although the researches of the past thirty years have demonstrated that it is almost without foundation.

In 1881 Dr. HERMAN ADLER[3] published the results of his long and careful studies, in which he gave the first real scientific evidence concerning the nature of the stimuli and character of gall formation. According to his results, the fluid secreted by the oak-gall fly is not irritating, and is not a factor in gall formation, but may serve as an antiseptic dressing for the wound in the plant. This view is strengthened by BEYERINCK,[4] who demonstrated that the fluid is without taste or smell and not irritating when injected under the skin. ADLER advanced the idea, which has been affirmed by other workers, that in the oak-gall flies, whatever irritating chemical exists comes from the larva and not from the parent insect. ADLER also reports his observation on *Nematus Vallismierii*, one of the saw flies, which attacks the *Salix amygdalina*. In this case the female pours out an abundant glandular secretion at time of oviposition, and the gall is well formed before the larva emerges from the egg.

It is also well known that mechanical stimuli will frequently cause abnormal growths. However, accurate data upon the results of various stimuli is not to be found in our literature.

ADLER says that the cecidia always originate from the formative cells of the plant, and that if the stimulation is applied to any other than the formative cells, cecidia are not produced. This statement opens up an enormous line of work. While some scale insects cause hypertrophies, others do not. Who has traced the ramifications of the mouth parts of these insects through the tissues of the host? Why do some Uredineae cause cecidia while other closely related species do not? Who has traced the mycelia of these related species

[3] Ueber den Generationswechsel der Eichengallen. Zeitschr. Wiss. Zool. **35**: 151–246. 1881. Translated in 1894 by CHARLES R. STRATON.

[4] Beobachtungen über die ersten Entwicklungsphasen einiger Cynipidengallen. Naturk. Verli. der Kon. Akad. Deel **22**:179. 1882.

in their ramifications through the tissues of the host plants? Who has solved the chemical and enzyme relationships which may exist between these fungi and their hosts? If the insect cecidia are the result of chemical stimuli, how about the myco-cecidia? If the insect cecidia are due to mechanical irritation, how about the myco-cecidia? If the insect cecidia are the result of irritation applied to the formative cells, is the same thing true for the myco-cecidia? By what school of biologists should these problems be worked? Will not the solution of one set help in the solution of others?

The writer is not presenting these questions for the purpose of controversy, but merely to call attention of students to this enormous field of plant pathology and plant physiology. Give us more data concerning the relationship between parasite and host plant, regardless of the character of the parasitic organism. Let us tear away the artificial barriers and give the broadest study to these problems.

DELAWARE AGRICULTURAL EXPERIMENT STATION
NEWARK, DELAWARE

AN ELECTRICAL CONSTANT TEMPERATURE APPARATUS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 151

W. J. G. LAND

(WITH FOUR FIGURES)

The temperature of incubators heated with gas taken directly from the mains is very irregular when an attempt is made to control the flow with mercury-actuated thermostats commonly used. Most mercurial thermostats will compensate for slight variations from the mean gas pressure, but not for large ones. The rise in temperature in the water-jacketed incubators used in the Hull Botanical Laboratory for paraffin infiltration was so sudden and so high that delicate plant tissues were often much distorted.

Electrically controlled heaters have been placed on the market recently by makers of repute, but the price of the apparatus ($50 and $100) is unreasonably out of proportion to the cost of material and labor.

In order to test the effect of definite temperatures on plant tissues for a longer time than is usually employed in imbedding, and having a direct current of 110 volts constantly on in the laboratory, the problem of devising a simple and efficient electrically controlled heater was first attacked about four years ago. The conditions of the problem were that the apparatus must maintain a definite temperature constant within very narrow limits for weeks at a time, must be easily adjustable to temperatures ranging from 40° C. to 80° C. with certainty, must be absolutely automatic in action, must be readily attachable to the usual type of ovens, must require practically no attention to keep in order, must be simple and inexpensive to construct, must use a minimum quantity of electricity, and must not be easily put out of adjustment by inexperienced or meddlesome persons.

For over two years the apparatus here described has replaced the gas heaters in this laboratory, with satisfactory results. The risk of fire, always great when gas is used, has been eliminated.

So many requests for information concerning the apparatus have been received that it has become impossible to give individual replies.

The apparatus consists of a metallic thermostat (fig. 1) placed on a shelf in the oven, a water-jacketed heating coil (fig. 2) fastened to the bottom of the oven in such a way that the water jacket of the coil forms a continuous system with that of the oven, and an automatic switch (fig. 3) placed wherever convenient.

The thermostat (fig. 1, *n*) is a thin strip of iron about 1 mm. thick and 2 cm. wide, firmly riveted to a strip of zinc the same width and

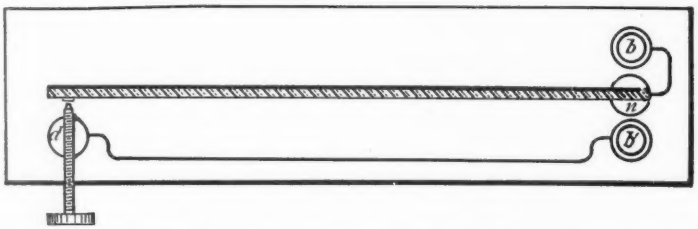


FIG. 1.—Diagram of thermostat and connections; *n*, thermostat of zinc and iron; *d*, screw for adjusting temperature; *b*, *b'*, binding posts to connect with *l*, *l'* of the switchboard.

from 1.5 mm. to 3 mm. thick. One end is fastened to a brass post set rigidly on the slate base, and the other end swings free. The free end of the metal tongue has a contact point of platinum fastened to the zinc side near the end. The adjustment for temperature is made with a platinum-tipped screw (*d*) set so that its point can always be brought in contact with the platinum disk on the metal tongue. The metal tongue and the adjusting screw are connected respectively with the binding posts (*b*, *b'*), as shown in the diagram.

The base of the thermostat should be made long enough to fit easily in the oven, the ends resting on ledges provided for the upper shelf. The sensitiveness of the thermostat depends, of course, on the length of the metal tongue. If extreme sensitiveness is required, it may be made nearly twice the length of the base and bent to a U, or it may be much longer and coiled. In practice 20 cm. has been found satisfactory. The zinc strip should not be thinner than

1.5 mm., or the thermostat will respond unpleasantly to any tremor of the bath or even in the laboratory building. If desired, brass or aluminium may be substituted for the zinc. The regulating screw should be made long enough to provide for quite a range of temperature. When the thermostat has been adjusted to the required temperature, it will need no further attention, except perhaps to brush the dust from the contact points at very long intervals. To raise the temperature turn the screw to the right, to lower it turn it to the left.

The heater (fig. 2) is a water-jacketed resistance coil of brass tubing and German-silver resistance wire. The tubing need not be thicker than 1 mm. The coil should be proportioned to the size of the oven it is intended to heat. For ovens having internal dimensions of 20×25×26.25 cm., and for temperatures of 30°–80°C., the size given here has been found suitable. Such a coil, however, will heat much larger ovens satisfactorily. The brass tubes should be about 15 cm. long. The resistance coil is four layers of no. 21 German-silver wire, wound on a tube 3 cm. *inside* diameter. The layers of wire are carefully insulated from the tube and from each other with asbestos paper about 0.6 mm. thick. The wire is wound with an engine lathe 24 turns to the inch under considerable tension, and the ends are brought out to binding posts (s, s') in the slate head of the coil. Wound as described, the current at 110 volts measures about 2.2 amperes.

The water jacket is made of 3 concentric brass tubes, the outer one being 6.25 cm. in diameter, the middle one 4.5 cm., and the inner one 3 cm. *outside* diameter, so that the tube of the heating coil will slip over it in close contact. The inner tube is closed at the lower end with a brass disk soldered tightly in place. The upper end remains open, and is fastened to the middle tube by a brass ring. The lower end of the middle tube is in turn fastened in a similar manner to the bottom of the outer tube. A hole is cut in the outer wall of the bottom of the oven, and the outer tube soldered directly to the bottom. If preferred, the outside tube may be threaded and screwed into a flange soldered to the bottom of the oven. If this method is used, a rubber gasket should be placed between the flanges, as shown in fig. 2. This arrangement

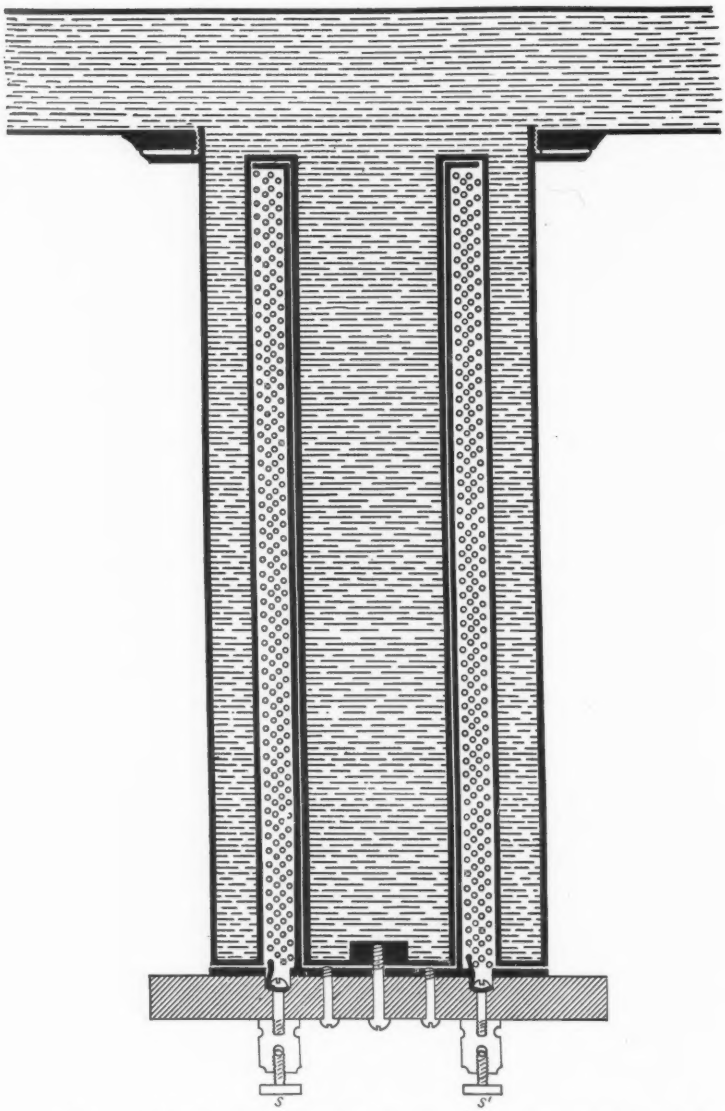


FIG. 2.—Median longitudinal section of heater, showing method of construction of water jacket and resistance coil, and how it is attached to the oven; s, s', binding posts to be connected with h, h' of the switchboard.

adds slightly to the cost, but will permit the sediment which appears in water-jacketed baths to be removed easily. Great care must be taken to have all joints absolutely water tight, since a leak will cause the destruction of the resistance wire in a few hours.

An inspection of the diagram (fig. 2) shows the arrangement is such that the resistance coil is completely surrounded by water except at the lower end, thus insuring rapid conduction of heat. Also the coil can be removed easily if repairs are ever necessary.

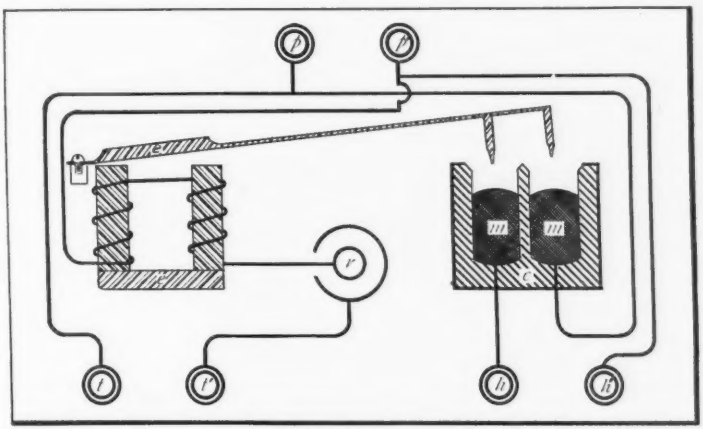


FIG. 3.—Diagram of automatic switch; *p*, *p'*, binding posts to connect with source of electrical supply; *e*, electromagnet; *a*, armature and switch; *r*, gasket for lamp rheostat; *t*, *t'*, binding posts to be connected with thermostat; *c*, container for mercury (*m*, *m*); *h*, *h'*, binding posts to be connected with heating coil.

In two years' use, only one has needed repairs, made necessary by spilling water on the head of the coil when the water jacket was being refilled.

The automatic switch (fig. 3) is a slate base having an electromagnet (*e*), armature (*a*) with switch, and a lamp rheostat (*r*) at one end, and the slate cups (*c*) filled with mercury at the other. A convenient size for the slate base is 20×11.25 cm. The magnets, which can be had very cheaply from electrical supply houses, should have a resistance of about 20 ohms. The armature (*a*) should be fastened by a spring to a pillar rigidly attached to the baseboard,

and should extend about 15 cm. to form the arm of the switch. Care must be taken not to have the spring too strong, or the armature will not be pulled down when the current flows through the coils of the magnet. The spring may be much weaker if an 8 or 4 candle power lamp is used instead of a 16 candle power lamp rheostat. One wire connects the post p directly to t; the other post p' is connected through the electromagnet e and the lamp rheostat socket r with t'.

The switch end of the armature should have two iron pins extending downward at a right angle, sharpened, and tinned to insure good contact with the mercury in the cups c. In practice it is advisable to drill two holes in the switch arm, tap them, and use iron machine screws for contact points. The screws should be provided with lock-nuts to hold them at the proper length. Switch points gradually wear away, due to the small arc which always occurs when contact with the mercury is broken. The machine screw device permits compensation for this wear. The screws should be sharpened of course, to minimize splashing, and tinned.

The double cup (c) for holding the mercury (m, m) should be made of slate. A convenient sized block is $5 \times 3.75 \times 2.5$ cm. The holes for mercury should have a diameter not less than 1.25 cm., preferably 2 cm., and the edges should be chamfered. The mercury oxidizes somewhat rapidly, and in consequence the volume should be rather large. Oxidation of the mercury is the chief defect of the apparatus, but no way has yet been found to prevent it. To compensate for oxidation, a small quantity of mercury must be added occasionally. One wire connects the post p with one of the mercury cups, the other cup is connected with h. The post p' is connected directly to h'.

The switch (fig. 3) may be put in any convenient place, preferably out of reach of inquisitive persons. Attach the heating coil (fig. 2) to the oven and place the thermostat (fig. 1) inside the oven on the upper ledges and connect the posts p, p' of the switch with any convenient lamp socket, fill the cups c with mercury, screw a lamp in the socket r, connect the posts t, t' with b, b' of the thermostat. Connect h, h' (fig. 3) with s, s' (fig. 2) of the heating coil. These connections are shown in fig. 4, a photograph of the apparatus.

It is realized that most botanists are not electricians, and therefore the description of the construction and wiring of the instrument is not written for experts.

The action of the apparatus is as follows: When the platinum points of the thermostat are in contact, the current flows through

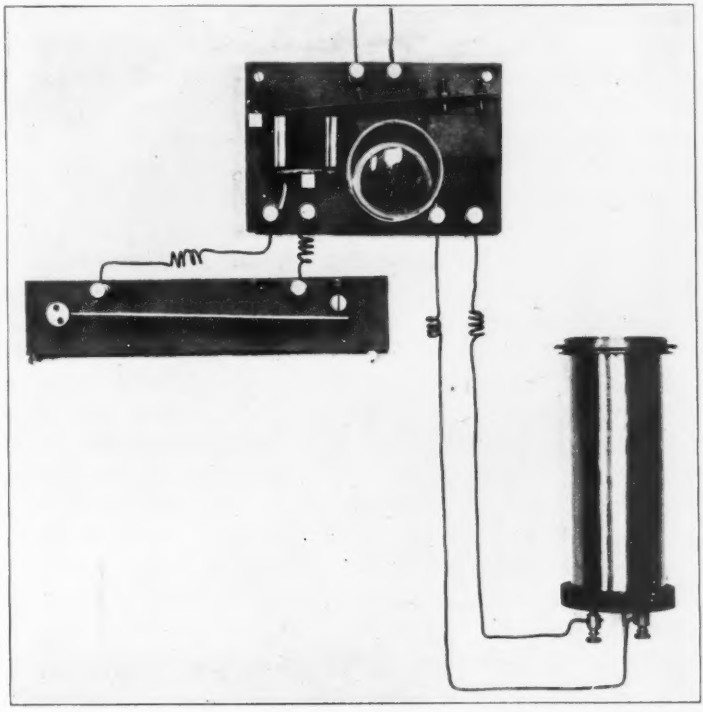


FIG. 4.—Photograph of thermostat, heater, and switch, with connections.

the electromagnet, the armature is drawn down, closing the switch and making a circuit through the heating coil. The circuit will remain closed only so long as the platinum points of the thermostat are in contact. As the temperature of the oven rises, the platinum points are separated, the circuit through the electromagnet is broken, and the switch is opened by the release of the armature.

When the temperature of the oven falls below the required point, the thermostat again functions and the switch is instantly closed. This action continues automatically as long as the current is supplied, or until the mercury in the cups is all oxidized. In one instrument it was found that a difference of 0.01° was sufficient to actuate the mechanism. As has been said before, turning the adjusting screw to the right adjusts for higher temperatures, and vice versa. It will be seen that the two circuits are absolutely independent of each other, and that when the oven is at the required temperature both circuits are broken; that the electricity is only on when the temperature is below the required point.

Because the switch closes so sharply when the thermostat functions, it is advisable to drill a small hole in the core of the magnet nearest the switch and insert a rubber plug for a buffer. If the mercury splashes too much, rubber corks, with a hole in the center, may be put in the tops of the cups. The flash which occurs when the switch points leave the mercury is bright, but it does no harm.

It is possible to use an alternating current, but it is very difficult to adjust the armature spring so as to avoid the unpleasant humming. It is planned to try a weighted or balanced armature with alternating currents. A battery may be used to actuate the switch if magnets of lower resistance are used, and the lamp rheostat replaced with a plug; then the alternating current may be used to heat the coil in the oven.

If preferred, the lamp used for a rheostat may be placed in the oven and connected to the socket on the switchboard with a cord and plug. This arrangement is very convenient, for the instant the door of the oven is opened the lamp is lighted. Also the heat of the lamp increases the efficiency of the apparatus.

Anyone at all familiar with tools can construct the apparatus at a cost of about $3.75 for material. Of course he must have access to an engine lathe to wind the coil so that the wires will not touch each other. After the first experimental instrument was found to work satisfactorily, the interest of a very expert mechanician, Mr. A. W. STRICKLER, 1311 E. 57th St., Chicago, Ill., was enlisted. He suggested many improvements, always having in mind increase of efficiency and lowering of cost. It is largely due

to his interest in the problem and his skill in construction that the apparatus has proved so efficient in this laboratory. He has recently devised a form of this thermostat which can be used with safety where explosive gases are present. He finds that when made as described here the cost should not exceed $15.00 for the apparatus complete and ready to attach to the incubator.

THE UNIVERSITY OF CHICAGO

BRIEFER ARTICLES

APOGAMY IN *PELLAEA ATROPURPUREA*

In the course of a study of fertilization and related phenomena in several ferns, a culture of *Pellaea atropurpurea* (L.) Link was found to have developed embryo sporophytes apogamously. The spores of this species were collected in October and sown on clay soil December 13, 1910. The soil was sifted into a small pot, moistened with water, and sterilized in an oven. The culture was kept under a bell jar in a Wardian case in the university greenhouse. Watering was found necessary but once, and was accomplished from below with distilled water.

The prothallia grew rather rapidly, and hundreds carefully examined at various times showed no indications of antheridia or archegonia. Two and one-half months after the spores were sown, the first indications were noticed of the development of apogamous embryos. Many prothallia were again examined on both surfaces for the appearance of sex organs, with negative results. On March 13, 1911, 110 prothallia were examined with special care; 47 bore sporophytes in various stages of development, but no sex organs were found in any case.

At an early stage in development it is difficult to distinguish between young antheridia and rhizoids. Young antheridia may be hidden among the rhizoids and escape attention; rhizoids, however, were in no case produced in great abundance in the culture in question. Thus the possibility is not excluded that rudimentary antheridia may have been formed; but my observations make it certain that none developed beyond the earliest stages, and that no archegonia were produced on these prothallia at any time.

The prothallia of this fern are of a darker green color than the prothallia of several other species in my cultures. They are generally heartshaped with a deeply cut notch, but many irregularly shaped prothallia occur. The first appearance of the apogamous embryo is indicated by a small darkened area usually a short distance back of the growing point. This, as sections made at this time show, represents a region of active division, the prothallial cells concerned being much

smaller than the neighboring ones which are not concerned in embryo formation. Embryos are formed on the inner sides of the lobes, as well as a short distance back of the apical notch. Long ribbon-shaped prothallia without apical notches also develop sporophytes at their distal ends. Sporophytes are often formed, therefore, in regions quite distinct from the meristematic area in which archegonia are ordinarily developed.

Soon after the beginning of embryo development, hairs appear surrounding the region of active growth. These originate from the area of the prothallium which is involved in the development of the embryo. Still later, the embryo projects from the prothallium, somewhat inclosed by the hairs, each of which is composed of several cells with large nuclei. As the embryo continues to grow, the primary leaf, from the petiole of which numerous hairs develop, makes its appearance. Later the primary root and stem are formed. At no time was there any evidence of the development of a structure which could be thought to correspond to a foot. In several cases two sporophytes began their development on the same prothallium. From studies so far made, it appears that both interior and surface cells of the prothallium are involved in the formation of the sporophyte.

During the present season, apogamous embryos have begun their development upon a large number of prothallia of this species in four cultures growing upon peaty soil. The first embryos were observed about one month after the sowing of the spores.

So far as I know, apogamy has not been previously reported in *Pellaea atropurpurea*, although WORONIN (1907) reported its occurrence in *P. flavens*, *P. nivens*, and *P. tenera*.—W. N. STEIL, *University of Wisconsin, Madison.*

CURRENT LITERATURE

BOOK REVIEWS

Vegetation der Erde

IX. Africa

As previously noted in these pages,[1] Engler has in contemplation an elaborate phytogeographic treatment of tropical Africa. The second volume of this series was the first to appear, and it is now followed by the first volume, which is issued in two parts.[2] The first volume is devoted to as much detail as is now possible to a consideration of the vegetational conditions of Africa. This volume makes it particularly clear that Africa is no longer the "unknown continent"; particularly is this true, so far as tropical Africa is concerned, of the German possessions, each of these being well delineated phytogeographically by maps in colors. Most of the volume is taken up by a presentation of the chief phytogeographical subdivisions of Africa, which, as here treated, are (1) Mediterranean Africa with the bordering parts of the Sahara, (2) tropical East Africa, (3) the southwestern region of winter rain, (4) the summer rain region of West Africa, (5) Macronesia. This portion of the work is richly and beautifully illustrated by photographs of desert landscapes in North Africa, cuts of representative Saharan plants, and by similar photographs and cuts in much greater number from tropical East Africa, including especially Abyssinia, the Somali Peninsula, and German East Africa. The account of the summer rain region of West Africa also is very full and is finely illustrated, especially in the portions dealing with the German territory. The work closes with a treatment of the general geographic conditions (including temperature and precipitation data, and an account of the various types of soils), a short description of the regions at different altitudes, a brief survey of the plant formations, and an account of the floral constituents and the general floristic relationships of Africa. Under the last head many genera are tabulated as to their affinities, whether pantropic, paleotropic, endemic, etc. Also there is a short account of the geological development of the present vegetation.

XI. The Balkan countries

Adamović, who for many years has published important papers dealing with the vegetation of Servia and neighboring lands, has now issued a mono-

[1] Bot. Gaz. **50**:468. 1910.

[2] Engler, A., und Drude, O., Die Vegetation der Erde. IX. Engler, A., Die Pflanzenwelt Afrikas insbesondere seiner tropischen Gebiete. Bd. I. pp. xxviii+1029. *maps 5. pls. 47. figs. 708.* Leipzig: Wilhelm Engelmann. 1910. *M* 60 (subscription *M* 45).

graph of the Balkan countries for the *Vegetation der Erde*.[3] After an account of the topography, hydrography, geology, and climate, there is a rather detailed treatment of the ecological factors, considerable attention being paid to the soil and to the plants which are confined to or are dominant on certain soils. Approximately half of the work is devoted to a consideration of the plant formations. Among the more interesting of these are such Mediterranean formations as (1) the mixed forests with the manna ash (*Fraxinus Ornus*); (2) the *Aesculus* forests; (3) the Sibljak formation, which is a type of thicket characteristic of the Balkan countries, including *Paliurus, Cotinus, Syringa*, and other representative forms; and (4) the Tomillares, a xerophytic formation, dominated by coarse herbs. On the hills and mountains there occur formations comparable to those of Central Europe, such as oak and chestnut forests, forests of *Pinus leucodermis* and *P. nigra*, fir forests, forest of *Picea Omorica*, beech forests, sand formations, mountain meadows, and mountain thickets. The third and fourth parts of the volume are devoted respectively to an account of the floristic composition and relationship of the region both horizontally and vertically, and to a developmental treatment of the Balkan vegetation from the Tertiary to the present. The region contains many interesting Tertiary relicts. In comparison with the ENGLER monographs on Africa, the Balkan volume is somewhat sparingly illustrated, and almost wholly by reproductions from photographs; the few illustrations, however, are excellently chosen.

XII. THE PERUVIAN ANDES

This volume is the second one of the series to treat of American vegetation. The general plan of the other volumes is followed, though the consideration is mainly floristic, very little being said regarding the formations.[4] WEBERBAUER, the author of the treatise, has spent several years of study in Peru, and is known to plant geographers by various papers dealing with Peruvian vegetation. Following the usual bibliography of literature and an account of the topography and climate, there is a survey of the plant families represented. Most of the volume is devoted to a detailed account of the vegetation by "zones," that is, by altitudinal subdivisions. These subdivisions are the Misti zone (2200–3400 m.) and the Tola zone (3400–4300 m.) on the western slope in southern Peru, the Loma zone of the coast, the northern desert zone, the central Sierra zone, the northern Sierra zone, the high

[3] ENGLER, A., und DRUDE, O., Die Vegetation der Erde. XI. ADAMOVIĆ, L., Die Vegetationsverhältnisse der Balkanländer (Möische Länder) unfassend Serbien, Altserbien, Bulgarian, Ostrumelien, Nordthrakien, und Nordmazedonien. pp. xvi+567. *maps 6. pls. 41. figs. 11.* Leipzig: Wilhelm Engelmann. 1909. *M* 40 (subscription *M* 30).

[4] ———, Die Vegetation der Erde. XII. WEBERBAUER, A., Die Pflanzenwelt der peruanischen Anden. pp. xii+355. *maps 2. pls. 40. figs. 63.* Leipzig: Wilhelm Engelmann. 1911. *M* 28 (subscription *M* 20).

Andes or Puna with its wonderful xerophytic forms, the eastern sclerophyll forests, the northern Paramo, and the luxuriant eastern tropical forests. This part of the work is rather fully illustrated by excellent cuts and photographic reproductions. A short section follows on the culture plants, the volume concluding with an account of the geological development of the Peruvian flora, mostly in the form of tabulations.—H. C. COWLES.

Plant life of Maryland

"The plant life of Maryland"[5] is the title of a volume issued as a Special Publication of the Maryland Weather Service, and is one of a series of reports of unusual completeness and excellence. The first of these reports dealt with the physiography and meteorology of the state; the second with the climate and weather of Baltimore and vicinity; and this, the third volume, presents the plant life in its relations to the physiography and climate, also inquires into the correlations between natural vegetation and crop possibilities, and includes the agricultural features and forest resources of the state.

The main part of the volume is by SHREVE, who directed the botanical survey. His introduction summarizes the geography, climatology, topography, mineralogy, and soils of Maryland. In Part II, after a brief history of field botany in the state, he discusses the floristics according to the present knowledge of the flora, comparing the three zones (coastal, midland, and mountain) with respect to the number and species of plants, and the floristic relations of the zones to each other and to other regions.

Part III occupies the body of the book and presents the ecological plant geography. SHREVE considers first the eastern shore district of the coastal zone under the several divisions: upland, swamp, marsh, aquatic, dune, and strand vegetation. Comparison of this district with the coastal plain of New Jersey and of the southern states brings out striking variations. CHRYSLER treats the western shore district of the coastal zone under the following topics: forests (upland, lowland, and cypress swamps), marshes (fresh and salt), peat bogs, strand, and cultivated plants, the chief interest being in his discussion of the succession of the forest types and in the transition of salt to fresh water marshes, this region affording unusual opportunities for such studies. In the lower district of the middle zone, the vegetation is classified by SHREVE according to the soil types, the topographical and general physical conditions being here uniform, and the vegetation less diversified than elsewhere. The upper district of the midland is divided into four natural belts of ridges and valleys, and the characteristic plant life of these divisions is discussed by BLODGETT. SHREVE describes the mountain zone under seven headings: slopes,

[5] SHREVE, FORREST, CHRYSLER, M. A., BLODGETT, FREDERICK H., and BESLEY, F. W., The plant life of Maryland. 4to. pp. 533. *pls.* 39. *figs.* 15. Baltimore: Johns Hopkins Press. 1911.

ridges, valleys, rocky slopes, glades, swamps, bogs, the topography determining in each case the character of the vegetation.

In Part IV, on the "Relation of natural vegetation to crop possibilities," SHREVE concludes that only in a general way may the native or introduced plant cover, as seen today, be significant of agricultural capabilities, although there is evidence that the virgin forest did give indication of the character of the underlying soil which was observed to advantage by the early settlers. Part V, on the "Agricultural features" by BLODGETT, Part VI on the "Forests and their products" by F. W. BESLEY, and Part VII, a "List of plants collected or observed" by SHREVE, complete the book.

The careful work of the authors and the collection of the floristic and ecological data make this a valuable treatise of its kind. It is handsomely printed and abundantly illustrated. For regions presented in such detail and with many local references, the lack of adequate maps is often noticed.—LAURA GANO.

MINOR NOTICES

Wettstein's Handbuch.—The mere fact that a second edition of a book has become necessary indicates that it has met some need. The second edition of WETTSTEIN'S *Handbuch*[6] does not differ essentially from the first edition. Minor inaccuracies have been corrected, additions have been made both from the rapidly increasing literature and from the author's own investigations, and a large number of illustrations, of the same high grade which made the first volume useful, have been added. As in the first edition, the work on angiosperms is particularly extensive, occupying about one-half of the entire book. This part of the work presents a compact, profusely illustrated account of all the more important families, which should give the beginner a sound foundation for advanced work, and which cannot fail to be helpful even to the professional taxonomist. It is encouraging to note that in discussing the phylogeny of angiosperms, the monocotyls are derived from the lower dicotyls.—CHARLES J. CHAMBERLAIN.

Ornamental shrubs.—It is safe to predict that the latest handbook by APGAR,[7] while intended for the general public, will prove most useful to the teaching botanist who has occasion to draw much of his material from parks and greenhouses. In its scope the volume includes not only native and hardy shrubs, but also introduced forms, many of which are conservatory plants in the northern United States. Numerous keys, based mostly upon leaf characters, appear to be most efficient in aiding the student to identify

[6] WETTSTEIN, R. V., Handbuch der systematischen Botanik. 2d edition. 8vo. pp. viii+914. *figs. 600.* Leipzig: Franz Deuticke. 1910. *M* 24.

[7] APGAR, AUSTIN C., Ornamental shrubs of the United States. 12mo. pp. 352. *figs. 621.* New York: American Book Company. 1910. $1.50.

species even when they are not in flower. The keys are supplemented by simple descriptions and by more than 600 illustrative drawings, while a glossary of botanical terms will prove useful to the beginner, and the size of the book will recommend it to all as a most useful pocket aid to the study of a comparatively unknown portion of our flora.—GEO. D. FULLER.

Dictionary of plant names.—GERTH VAN WIJK,[8] a teacher in the schools of Holland, has published the result of a most laborious compilation of data, extending through twenty-five years. The dictionary is intended to enable one to find the vernacular name of a plant in four languages, provided he knows its scientific name; the four languages chosen being English, French, German, and Dutch. Two other parts are promised, which will really form an index to the first parts, and will enable one to find the scientific name of a plant if he knows the vernacular name in any one of the four languages. All questions as to the usefulness of such a work are submerged by amazement at this exhibition of enjoyment in endless drudgery.—J. M. C.

Album of thallophytes.—The first fascicle of an album of the algae, fungi, and lichens, by COUPIN,[9] indicates that the complete work will be useful to all who are interested in the lower plants. All the genera and many of the more important species are illustrated by drawings emphasizing the features which are of importance in classification. The figures are in plates opposite the descriptions, and with the description of each species is a bibliography of the principal contributions, so that more extended information may be easily obtained.—CHARLES J. CHAMBERLAIN.

Natürlichen Pflanzenfamilien.—Parts 241 and 242 conclude the supplement to the Chlorophyceae by N. WILLE; include that to the Phaeophyceae and Dictyotales by the late F. R. KJELLMAN and N. SVEDELIUS; and begin the supplement to the Rhodophyceae by N. SVEDELIUS, who continues it in parts 243 and 244. A new genus (*Pseudolithoderma*) of Lithodermataceae is described by SVEDELIUS.—J. M. C.

NOTES FOR STUDENTS

Current taxonomic literature.—O. AMES (Phil. Journ. Sci. Botany **6**:35–56. 1911) under "Notes on Philippine orchids with descriptions of new species III" places on record additional data concerning this group of plants in the Philippines and describes 22 species new to science.—R. C. BENEDICT (Am. Fern Journ. **1**:40–42. *pl. 2.* 1911) describes and illustrates a new species of

[8] GERTH VAN WIJK, H. L., A dictionary of plant names. 2 parts. 4to. pp. xxiv+1444. Haarlem: Published by the Dutch Society of Sciences. 1909, 1910.

[9] COUPIN, HENRI, and COUPIN, MLLE. FERNANDE, Album générale des Cryptogames (algues, champignons, lichens). Fasc. 1. *pls. 1–15.* Paris: E. Orlhac, Editor. *fr.* 2.50.

Anemia (*A. nipeënsis*) from Cuba. The same author (Bull. Torr. Bot. Club **38**:153–190. *pls. 2–8.* 1911) presents the results of studies in the fern tribe *Vittarieae*, recognizing 7 genera. Several new combinations are made and one new species of *Polytaenium* (*P. quadriseriatum*) is described from Hayti.—E. BETHEL (Mycologia **3**:156–160. *pl. 48.* 1911) describes and illustrates a new species of *Gymnosporangium* (*G. Kernianum*) from Colorado.—E. BICKNELL (Bull. Torr. Bot. Club **38**:103–133. 1911) in continuation of his studies on "The ferns and flowering plants of Nantucket" recognizes 12 species of *Rubus* and characterizes 24 hybrids in this genus.—F. BORGESEN (Bot. Tidsskir. **30**:177–207. 1910) under the title "Some new or little known West Indian Florideae II" has published critical notes on several species of the region, describes two species new to science, and proposes a new genus (*Coelarthrum*), based on *Chylocladia Albertisii* Piccone.—F. BRAND (Ber. Deutsch. Bot. Gesells. **29**:138–145. *pl. 7.* 1911) has described several new green algae collected by MISS J. E. TILDEN in New Zealand. One new genus (*Rhytisiphon*) of the Siphoneae is proposed.—A. BRESADOLA (Med. Rijks. Herb. pp. 75, 76. 1911) has published 4 new species of Polyporaceae, two of which (*Fomes subendothejus* and *F. surinamensis*) are from South America.—F. BUBÁK (Ber. Deutsch. Bot. Gesells. **29**:70–74. 1911) in an article entitled "Eine neue Krankheit der Maulbeerbäume" describes a new genus (*Dothiorellina*) from Bulgaria. The fungus is parasitic in the branches of *Morus alba*.—L. BUSCALIONI (Ann. Botany **9**:87–122. *pls. 1–4.* 1911) records several species of the Sympetalae from the region of the Amazon in Brazil and describes and illustrates new species in the following genera: *Torenia*, *Drymonia*, and *Memora*.—C. DE CANDOLLE (Rep. Nov. Sp. **9**:229–235. 1911) has published 11 new species of *Piper* from Bolivia.—A. CHASE (Proc. Biol. Soc. Wash. **24**:103–160. 1911) presents the results of further studies on the Paniceae, and includes a new species in the genus *Valota* and two in *Axonopus*. Two new genera are proposed, namely, *Homolepis*, based on *Panicum aturense* HBK., and *Scutachne*, based on *Panicum durum* Griseb.—T. F. CHEESEMAN and H. B. HEMSLEY (Kew Bull. 188, 189. 1911) have published a new genus (*Coxella*) of the Umbelliferae; the genus is founded on *Ligusticum Dieffenbachii* Hook. f.—E. CHIOVENDA (Ann. Botany **9**:51–85, 125–152. 1911) under the title "Plantae novae vel minus notae e regione aethiopica" has published several species of flowering plants and proposes the following new genera: *Tzellemtinia* of the Rhamnaceae, *Hymenosicyos* of the Cucurbitaceae, *Erythroselinum* and *Stephanarossia* of the Umbelliferae, and *Petrollinia* of the Compositae.—R. CHODAT (Bull. Soc. Bot. Genève II, **3**:125, 126. 1911) has described a new genus (*Ernstiella*) of the Myxophyceae. The alga was found in one of the parks of Geneva.—H. N. DIXON (Journ. Bot. **49**:137–150. *pl. 513.* 1911) has published several new species of Indian mosses and includes a new genus (*Hyophilopsis* Card. and Dixon) of the Pottiaceae.—S. T. DUNN (Kew Bull. 193–198. 1911) has published a new genus (*Adinobotrys*) of the Leguminosae and refers thereto four species from the Indo-Malayan region and

China. The same author in cooperation with DR. HARMS (Journ. Bot. **49**: 106–109. 1911) has proposed a new genus (*Craibia*) of the Leguminosae. The genus, as here treated, embraces nine species of trees, all of African distribution.—C. W. EDGERTON (Phytopathology **1**:12–17. *pl. 4.* 1911) under the title "Two new fig diseases" records two fungi found on the fig tree at Baton Rouge, Louisiana, one (*Tubercularia Fici*) being new to science.—A. ENGLER (Bot. Jahrb. **46**:1–288. *pls. 1–4.* 1911) under the general title of "Beiträge zur Flora von Afrika XXXVIII," in cooperation with several noted specialists, publishes an important contribution to our knowledge of the flora of Africa. About 160 species are here published for the first time, and one new genus (*Simarubopsis*) of the Simarubaceae from central Togo is described and illustrated. The paper includes a synoptical revision of the African species of *Ficus* by J. MILBRAED and M. BURRET. These authors recognize 95 species of this genus from Africa, and a key precedes their enumeration.—A. J. EWART, J. WHITE, and B. WOOD (Proc. Roy. Soc. Victoria, N.S. **23**²:285–304. *pls. 49–57.* 1911) under "Contributions to the flora of Australia, No. 16" have described several species new to science and propose a new genus (*Sarga* Ewart) of the Gramineae.—C. E. FAIRMAN (Ann. Mycol. **9**:147–152. 1911) under the heading "Fungi Lyndonvillenses novi vel minus cogniti" has published 8 new species of fungi from the vicinity of Lyndonville, New York.—C. FERDINANDSEN amd O. WINGE (Bot. Tidsskr. **30**:208–222. 1910) record several species of fungi obtained on the WARMING expedition to Venezuela and the West Indies in 1891–92. A new species is added to *Helotium* and one to *Sterigmatocystis*. Two new monotypic genera are characterized, namely, *Myxotheca*, found on the pinnae of *Trichomanes pinnatum* from the island of Trinidad, and *Stilbochalara*, found on decaying fruits of cacao from Venezuela.—W. O. FOCKE (Rep. Nov. Sp. **9**:235–237. 1911) records 5 new species of *Rubus* from Central and South America.—R. E. FRIES (*ibid.* 211) has published a new species of *Wissadula* (*W. indivisa*) from Paraguay.—E. L. GREENE (Leafl. Bot. Obs. and Crit. **2**:121–152. 1911) has described upwards of 50 new species of flowering plants chiefly from western United States. One new genus (*Sandbergia*) of the Cruciferae is proposed. The same author (Am. Mid. Nat. **2**:73–90. 1911) under the heading "*Antennaria* in the Middle West" recognizes 13 species of this genus from the central part of the United States; of this number 7 are said to be new. A key to the species precedes their description.—R. M. HARPER (Torreya **11**:64–67. 1911) records a new *Prunus* (*P. geniculata*) from Florida.—L. L. HARTER (Mycologia **3**:154, 155. 1911) has published a new species of *Alternaria* (*A. Forsythiae*) found at Washington on living leaves of *Forsythia suspensa* Thunb.—E. HASSLER (Rep. Nov. Sp. **9**:145–160, 193–197. 1911) has published several new species and varieties of Leguminosae and Convolvulaceae from Paraguay.—F. HEDGES (Phytopathology **1**:63–65. *pl. 15.* 1911) describes and illustrates a new fungus (*Sphaeropsis tumefaciens*) from Jamaica; this fungus is said to be "the cause of the lime and orange knot."—F. HEYDRICH (Ber. Deutsch. Bot. Gesells.

29:26–33. *pl. 2.* 1911) in an article entitled "Die Lithothamnien vor Roscoff" describes and illustrates a new genus (*Squamolithon*).—R. H. HOWE, JR. (Mycologia **3**:106–150. *pls. 41–47.* 1911) under the title "American species of *Alectoria* occurring north of the fifteenth parallel" recognizes about a dozen species and records a new one (*Alectoria pacifica* Stzb.) from the Island of Guadalupe off the California coast.—G. KÜKENTHAL (Philip. Journ. Sci. Bot. **6**:57–64. 1911) gives a synopsis of the Philippine *Caricoideae*, with a key to the species of *Carex*, 24 being listed for the Philippines, one (*C. pycnothyrsos*) hitherto unknown to science.—J. LUNELL (Am. Mid. Nat. **2**:57–60. 1911) records 4 new species of Compositae from North Dakota, and (*ibid.* 90–94) under the title "New plants from North Dakota" characterizes 8 varieties of "*Laciniaria scariosa.*"—B. MACKENSEN (Bull. Torr. Bot. Club **38**:141–143. 1911) records 2 new species of *Opuntia* from Texas.—W. A. MURRILL (Mycologia **3**:97–105. *pl. 40.* 1911) in the eighth article on "Illustrations of fungi" describes and illustrates several plants and records new species in *Omphalia*, *Inocybe*, and *Campanularius.*—J. A. NIEUWLAND (Am. Mid. Nat. **2**:60–65. 1911) in an article entitled "The type of the genus *Panicum*" proposes a new generic name *Chasea*, and transfers thereto several species of *Panicum*. *Panicum clandestinum* L. is taken as the type of the newly constituted genus.—L. O. OVERHOLTS (Ohio Nat. **11**:353–373. 1911) under the heading "The known Polyporaceae of Ohio" records 118 species from that state.—A. PASCHER (Ber. Deutsch. Bot. Gesells. **29**:112–125. *pl. 6.* 1911) gives an account of a new tentacle-bearing chrysomonad, found growing in ditches on *Mikrospora* and *Oedogonium* at Franzensbad, Germany. The plant has been designated by the generic name *Cyrtophora* and together with *Pedinella* Wyssotzki and *Palatinella* Laut. are referred to a distinct family Cyrtophoraceae.—F. PETRAK (Rep. Nov. Sp. **9**:177, 178. 1911) has published a new species of *Cirsium* (*C. Greenei*) from northern Mexico.—J. A. PURPUS (Monats. für Kakteenk. **21**:50–53. 1911) describes and illustrates a new species of *Mamillaria* (*M. Sartorii*) from Mexico.—C. B. ROBINSON (Philip. Journ. Sci. Bot. **6**:1–33. *pls. 1–3.* 1911) presents the concluding article in his consideration of the "Philippine Urticaceae." In this paper 11 genera are recognized and to them are referred 43 species of which 13 are new. A new genus (*Astrothalamus*) is proposed, which is based on *Maoutia reticulata* Wedd.—H. H. RUSBY (Bull. Torr. Bot. Club **38**:145, 146. 1911) describes a new species of *Mayepea* and one of *Morus* from Mexico.—R. SCHLECHTER (Rep. Nov. Sp. **9**:161–166, 212–218, 281–287, 289–294. 1911) under the title "Orchidaceae novae et criticae" has published new species of orchids from different parts of the world, including several from Mexico and Central America. One new genus (*Solenocentrum*) is proposed from Costa Rica.—P. C. STANDLEY and J. C. BLUMER (Muhlenbergia **7**:44–47. *pl. 5.* 1911) have described and illustrated a new species of *Castilleja* (*C. austromontana*) from the southern Rocky Mountains.—J. STEINER (Oesterr. Bot. Zeits. **61**:177–183. 1911) had published several new species of lichens, including one (*Buellia mexicana*) from Mt.

Hinatikatl, Central America.—G. S. WEST (Journ. Bot. **49**:82–89. 1911) under the heading "Algological notes" characterizes a new genus (*Oligochaetophora*); the genus is based on *Polychaetophora simplex* West, which was found originally growing on submerged portions of various aquatic flowering plants at Donegal, England.—J. M. GREENMAN.

Cecidology.—Among the most important of the recent papers on galls is that by DENIZOT[10] on the gall of *Andricus radicis*. This gall occurs on the roots of at least three species of oaks, and appears to resemble somewhat the American twig gall caused by *A. punctatus* Bassett. The gall is plurilocular, but its histological structure is very similar to the unilocular gall caused by *A. sieboldi*. The gall is made up primarily of parenchyma tissue, and each larva is surrounded by a definite structure as follows: (1) a zone of parenchyma tissue well filled with starch and known as the nutritive zone; the starch disappears with the growth of the larva and is supplanted by tannin and oil; (2) a protective zone of sclerenchyma tissue containing albuminoids and tannin. There is a gradual transition between these two zones. The superficial part of the gall is made up primarily of cork cells whose contents are reduced to a thin layer of tannin deposited against the inner walls. The tannin exists in all parts of the gall, but is most abundant in the parts referred to above, and increases in amount with the decrease in starch. It causes a coagulation of the contents of the cells, persisting in the protective cells in the form of grains, and in the cork cells as a thin peripheral layer. The reviewer has observed similar conditions in several of our American galls.

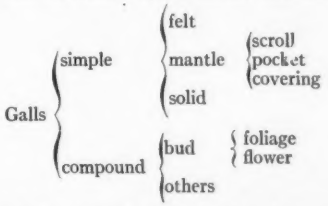
Another exceptionally good piece of work is that of HOUARD[11] on the action of certain scale insects on the plant tissues. His studies were restricted to *Asterolecanium variolosum*, *A. thesii*, and *A. algeriense* on *Quercus peduncularia*, *Q. sessiliflora*, *Q. pubescens*, *Pittosporum tobira* (an Asiatic plant), *Templetonia retusa* (an Australian plant). In all cases these insects cause cone-shaped swellings, and in the tip of each cone a depression in which the insect is located. The swellings are due partly to thickening of the bark and partly to a modification of the vascular bundles. The galls differ in accordance with the response of the vascular bundles to the stimulating influences of the insects; the more compact the bundle, the greater the resistance. If the bundles are compact, the hypertrophy of the medullary rays is slight and the bundles only slightly separated, thus making it difficult for the parasite to reach any great depth. In the case of *A. variolosum*, the vascular bundle responds to the action of the insect in the formation of new wood only. This new wood possesses an abnormal structure due to the sucking of the insect interfering with the normal differentia-

[10] DENIZOT, M. GEORGES, Sur une galle du chêne provoquée par *Andricus radicis* (Cynipide). Rev. Gén. Botanique **23**:165–175. 1911.

[11] HOUARD, C., Action de Cécidozaires externes, appartevant au genre *Asterolecanium*, sur les tissues de quelques tiges. Marcellia **10**:3–25. 1911.

tion of the fibers. The major part of this abnormal structure forms lignified cells with slightly thickened walls. In the case of *T. retusa*, the ring of vascular bundles presents enough resistance to prevent the hypertrophy of the medullary rays. However, *A. algeriense* has a stronger influence on the intermediate woody vessels, stopping their development and causing a hypertrophy of the thickened angles of the stem. The vascular bundles in the stem of *P. tobira* are much less resistant than in any of the preceding host plants; in this case the insect affects the bark, easily gains entrance to the medullary rays, and causes a hypertrophy which results in the separation of the vascular bundles. The modification of the tissues between the bundles is advantageous to the insect. In the petioles and midribs, the bundles do not form a complete ring and therefore are much less resistant than in the twigs, and are subject to much greater hypertrophy. In all cases, except the last, the external tissues of the stem undergo excessive hypertrophy and form the greater part of the gall.

The biology of galls is ably discussed by DR. ARTUR MODRY,[12] who gives a review of the subject and also the results of his own investigations. Although the study of galls is very old, it has attracted comparatively little attention from biologists. The workers on this subject have defined galls differently, but the definition given by BEYERINCK is most generally accepted at the present time. According to this definition, the gall is a "new formative growth within the body of the plant and is due to insects or plant organisms." THOMAS suggested the use of the word "cecidien" (meaning nut gall) as a substitute for all other terms; then subdivided the galls on basis of cause into Phyto-cecidien and Zoo-cecidien, and these groups into myco-, helminto-, phytopto-, entomo-cecidien, etc. Although this marked an advance in the study of cecidology, it was of very little botanical importance. This was largely overcome by KERNER,[13] who suggested the following divisions:



This division has been of great value for descriptions. In 1904 ROSS suggested division into root, stem, leaf, and blossom galls. This division has been of considerable value, but was not very practical. LACAZE-DUTHIERS (1849–1853) suggested division into internal, external, and mixed galls. However, the greatest advance was made by KÜSTER, who as a result of his study

[12] MODRY, DR. ARTUR, Beiträge zur Gallenbiologie. Sechzigsten Jahresb. K.K. Staats-Realschule. 1911.

[13] KERNER AND OLIVER, The natural history of plants 2:514–554. 1895.

of gall anatomy divided them into (1) galls without cell multiplication (enlargement of cells should not be confused with multiplication of cells), (2) soft galls, and (3) hard galls. The divisions are based on the character of the tissues of which the galls are composed. The author admits there are so many intermediate stages as to make these divisions in some cases very unsatisfactory. MODRY follows KÜSTER'S divisions, and gives a very comprehensive review of the various structural (both external and internal) characters of the various groups of zoo-cecidia. A review of this part of the paper would require entirely too much space and is entirely unnecessary for those who are familiar with the literature of the histology of galls.

Another paper of great interest to Americans is by TROTTER[14] on a collection from Washington, Oregon, Arizona, California, Hawaii, and Mexico. In this paper the author describes 88 species, of which 9 have been described. Of the remaining 79, 13 are given specific names and the remainder assigned to genera only. This paper is a most excellent illustration of our lack of knowledge of the American cecidia.

Dr. SCALIA[15] gives a very interesting discussion and description of a new species on *Cyclamen neapolitanum*, to which he assigns the name *Phyllocoptes Trotteri*.

One of the most valuable contributions to American cecidology in recent years is SMITH'S[16] paper on crown gall and sarcoma. In his recent bulletin on crown gall, Dr. SMITH calls attention to the resemblances of crown gall of plants to malignant animal tumors, especially to sarcoma. This resemblance has attracted the attention of many workers, but it remained for SMITH to demonstrate that it is something more than superficial. The questions previously unsolved which SMITH answers are (1) the presence of bacteria in the secondary tumors, (2) the origin of the secondary tumor from the primary to which it remains attached by strands of tumor tissue, (3) the structure of the secondary tumor is the same as that of the primary. The strand of tumor tissue connecting the galls works its way as an outgrowth from the primary gall, through the interior of the stem and leaves. At suitable places it undergoes enlargements, forming deep seated secondary galls which eventually become apparent on the surface. These tumor strands contain the bacteria which cause the disease. We are promised another bulletin on this interesting subject which we will await with great interest.

Another very interesting contribution, which the reviewer believes should

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[14] TROTTER, A., Contributo alla Conoscenza delle Galle dell America Nord. Marcellia **10**:28–61. *pl. 1. figs. 21.* 1911.

[15] SCALIA, DR. C., Nuova Species di Eriofide sul *Cyclamen neapolitanum* Ten. Marcellia **10**:62–64. 1911.

[16] SMITH, ERWIN F., Crown gall and sarcoma. Circular No. 85. U.S. Bureau of Plant Industry. 1911.

be included under cecidology, is that part of the work of EAST and HAYES[17] on inheritance in maize which refers to "plant abnormalities." In this part of the work, the authors state their objects as follows: "The first object was to see whether the manner of transmission of inheritable monstrous characters gives any clue to the reason why monstrosities have seldom obtained a foothold in nature when in competition with normal types. The second object was commercial. If teratological specimens appear in commercial varieties of maize, it is desirable to know the easiest method to destroy them." The authors discuss the appearance of and experiments with dwarf forms, irregularity of rows of seeds on cob, bifurcated ears, ears with lateral branches, plants with striped leaves, and hermaphrodite flowers. They call attention to the fact that many of these monstrous variations occur in strains that have been self fertilized for several generations, and suggest that inbreeding may give the same effect as lack of nutrients, while cross-breeding may give the opposite effect. Monstrosities are due to retardation or acceleration of cell divisions. The question is then raised as to whether the monstrosities might not be due to an abnormal distribution of the chromatin. Another paper is promised on the effects of inbreeding in maize.—MEL. T. COOK.

Recent papers on Phytomyxaceae.—MAIRE and TISON[18] have published a brief note on *Tetramyxa parasitica* Goebel, which produces galls on *Ruppia* and *Zannichellia*. The parasite appears in the host cell in the form of an amoeba, which undergoes division simultaneously with the host cell in such a way that at first only a single amoeba appears in each cell. During this stage the nuclei are said to divide in the manner described by NAWASCHIN and by PROWAZEK for *Plasmodiophora*. As these accounts differ somewhat as to detail, it may be inferred that the division in its main features follows the method common to the members of this group, by the formation of a chromatic ring around a karyosome, both of which divide. This stage is followed by the chromidial stage, during which the chromatin disappears from the nuclei and chromatic bodies appear in the protoplasm. Later the (same) nuclei appear with a chromatin network and undergo two karyokinetic divisions, which are followed by spore formation. Karyogamy was not observed.

In a second paper, MAIRE and TISON[19] describe a new genus, *Ligniera*, to include those species of the Plasmodiophoraceae which lack the schizogenous stage or have it very poorly developed, and which do not cause gall formation in the host plant. By these characteristics the genus is separated from the genera

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[17] EAST, E. M., and HAYES, H. K., Inheritance in maize. Conn. Agric. Exp. Station, Bull. 167. pp. 129–137. 1911.

[18] MAIRE, RENÉ, et TISON, ADRIEN, Sur quelques Plasmodiophoracées. Compt. Rend. **150**: 1768–1770. 1910.

[19] ———, Sur quelques Plasmodiophoracées non hypertrophiantes. Compt. Rend. **152**: 206–208. 1911.

Plasmodiophora, *Sorosphaera*, and *Tetramyxa*. The new genus includes *L. radicalis*, which is new, *L. Junci* (Schwartz) (*Sorosphaera Junci* Schwartz), and *L. verrucosa*, also new.

OSBORN[20] gives an account of the development of the interesting form *Spongospora subterranea*, causing the corky scab of potatoes. Penetration of the organism into the host cell was not observed, nor was it possible to infect sound potatoes with spores. The first stage observed consisted of an amoeba containing a single nucleus, which had a membrane, chromatic granules, and a deeply staining karyosome. In the early stages nuclear division is followed by division of the amoeba, so that a number of independent amoebae are found in the same host cell. The parasites occur in the cambium, and when the parent cell divides, one or more amoebae are included in each daughter cell, in the manner described by NAWASCHIN for *Plasmodiophora*, and by BLOOMFIELD and SCHWARTZ for *Sorosphaera*. The division of the nuclei during this stage is of the type characteristic of the group. The chromatin forms a ring around the karyosome; both the ring and the karyosome then divide, and the halves move toward the poles, where the halves of ring and karyosome unite into a deeply staining mass. The nuclear membrane constricts between the masses, and finally divides at the point of constriction, leaving each chromatic mass enclosed in a separate membrane. No fibers or polar radiations were observed. At a later stage many of the amoebae are multinucleate, and when the food content of the host cell is exhausted, the amoebae coalesce to form a plasmodium. At this time the chromatin of the nuclei disappears and chromatic material appears in the protoplasm. When the nuclei appear organized again, they contain a chromatin network but no karyosome. The author is inclined to believe that the new nuclei are constructed *de novo*. This stage is soon followed by fusion of nuclei in pairs, and a period of nuclear growth previous to spore formation. Two karyokinetic divisions take place, after which the protoplasm is rounded up into uninucleate spores.

In a later paper MAIRE and TISON[21] give the results of further observations on *Sorosphaera*, *Tetramyxa*, *Ligniera*, and *Mollierdia*, some of which differ in some points of their development from other forms of this group. *Tetramyxa parasitica* has multinucleate plasmodia during the phase representing the schizogenous stage, the nuclear divisions not being accompanied by cell division. The chromidial stage, prominent in other forms, is lacking here. At the beginning of spore formation, the plasmodia break up into uninucleate masses. These masses become four-nucleate as a result of two mitotic divisions, and divide by constriction into four uninucleate spores. In this form, as

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[20] OSBORN, T. G. B., *Spongospora subterranea* (Wallroth) Johnson. Ann. Botany **25**:327–341. *pl. 27*. 1911.

[21] MAIRE, RENÉ, et TISON, ADRIEN, Nouvelles recherches sur les plasmodiophoracées. Ann. Myc. **9**:226–246. *pls. 10–14. fig. 1*. 1911.

well as in *Sorosphaera*, amoebae are carried into new cells by the division of the infected host cell as described above for *Spongospora*.

Ligniera radicalis develops in the root hairs and cortical parenchyma of the roots of *Callitriche stagnalis*. As stated in the former paper, a true schizogenous phase is lacking. As in *Tetramyxa*, cell division does not accompany nuclear division during the growth of the organism. The chromidial stage occurs here as usual before the meiotic divisions. The first of these divisions often occurs before the plasmodium has broken up, but in such cases the plasmodium breaks up into "energids" during the second mitosis in such a way that the four nuclei resulting from the two mitoses are inclosed in the protoplasmic masses, which break up into four spores. The mode of development of *L. Junci* and *L. verrucosa* is similar to that of *L. radicalis*.

Molliardia is described as a new genus to include *Tetramyxa Triglochinis* Molliard. This form is peculiar in producing no spores on the host plant. The infected cells contain plasmodia which soon break up into uninucleate schizonts. These become 2–8-nucleate and break up anew. The full life history of this form is not known. In conclusion, the author adds some observations on the affinities of the Plasmodiophoraceae. He is inclined to regard them as being more closely related to such forms as *Rhizomyxa* and *Woronina* among the Chytridiales than to the Myxomycetes.—H. HASSELBRING.

The Grigna mountains.—The Grigna group of mountains includes some 60 square miles of mountainous country in northern Italy, adjoining the eastern shores of Lake Como and the connecting Lake Lecco. Its phytogeographical description by GEILINGERE[22] has an additional American interest because of the location of the region near the main route of American tourist travel. Notwithstanding its small area, the elevation varies from 199 meters at Lake Como to 2,410 meters on the highest of the peaks. This permits a wide range in climate, which is of course reflected in the vegetation. The Mediterranean province does not reach so far north, but many species of Mediterranean origin are present, and the olive extends to a maximum altitude of 490 meters. Most of the area is comprised within the submontane region, with forests of oak, hop hornbeam, and chestnut extending up to 1050 meters. From this elevation to 1650 meters the montane beech forests dominate. These in turn are succeeded by the subalpine forests of larch as far as 1950 meters, above which is the treeless alpine region. For all of these regions the author distinguishes ecological groups with a detail seldom approached in America. He recognizes seven chief types of vegetation, including forest, bush-forest, perennial herbs, grassland, swamps, aquatic vegetation, and rock vegetation. These are subdivided into formational groups, formations, and societies, of successively minor importance. This classification is based

[22] GEILINGERE, G., Die Grignagruppe am Comersee. Bot. Centralbl. **24**²: 119–420. 1909.

primarily upon physiognomy, and only secondarily upon environment or floristic composition. It is doubtful whether such a method can ever give entirely satisfactory results, although the author considers it the best for this region, where all the associations show the effect of cultural changes. Probably the gravest defect of the paper is the entire failure of the author to discuss the dynamics of the vegetation. The development of the various associations and their successional relations are omitted completely. Illustrations would have added greatly to the clearness of the descriptions, and the scale of the accompanying map would have easily permitted the location of the chief types of vegetation. Almost half of the lengthy article is occupied by a carefully annotated list of species.—H. A. GLEASON.

Gametophytes and embryo of Pseudolarix.—MIYAKE and YASUI[23] have investigated the monotypic *Pseudolarix* (*P. Kaempferi*), a native of China, one of the Abietineae whose morphology had not been studied. The material was obtained from a tree growing in a garden in Pallanza, Italy. The winged pollen grains contained the usual cells of the male gametophyte, and the divisions showed 12 chromosomes, but the later development of the gametophyte was not seen. Megaspore formation was observed, a linear tetrad being formed about the time of pollination (April in Italy). The large central vacuole is formed in the spore stage (before free nuclear division), and the young female gametophyte is invested by several layers of nutritive cells. At maturity, the megaspore membrane is well developed, as in other Abietineae. Early in June the female gametophyte is solid tissue, and then the 5 or 6 archegonium initials appear, the archegonia maturing in about three weeks. After the division of the central cell, the ventral canal cell disorganizes at once. Fertilization occurs about the end of June, and the first four free nuclei of the proembryo move to the base of the egg, walls appearing with the next division. The cells of each tier divide, and the completed proembryo consists of four tiers, with four cells in each tier. The functions of the tiers are as in *Pinus*, and the whole situation seems to be an almost exact duplication of that genus.—J. M. C.

A cedar bog in Ohio.—DACHNOWSKI[24] records, as an isolated area of northern plants, left behind in the great northward migrations following upon the retreat of the ice sheet of the glacial period, a swamp in central Ohio, characterized by *Thuja occidentalis* and other species not usually found south of central Michigan. Mats of sphagnum, together with the sundew and various orchids, testify to the true bog character of the association.—GEO. D. FULLER.

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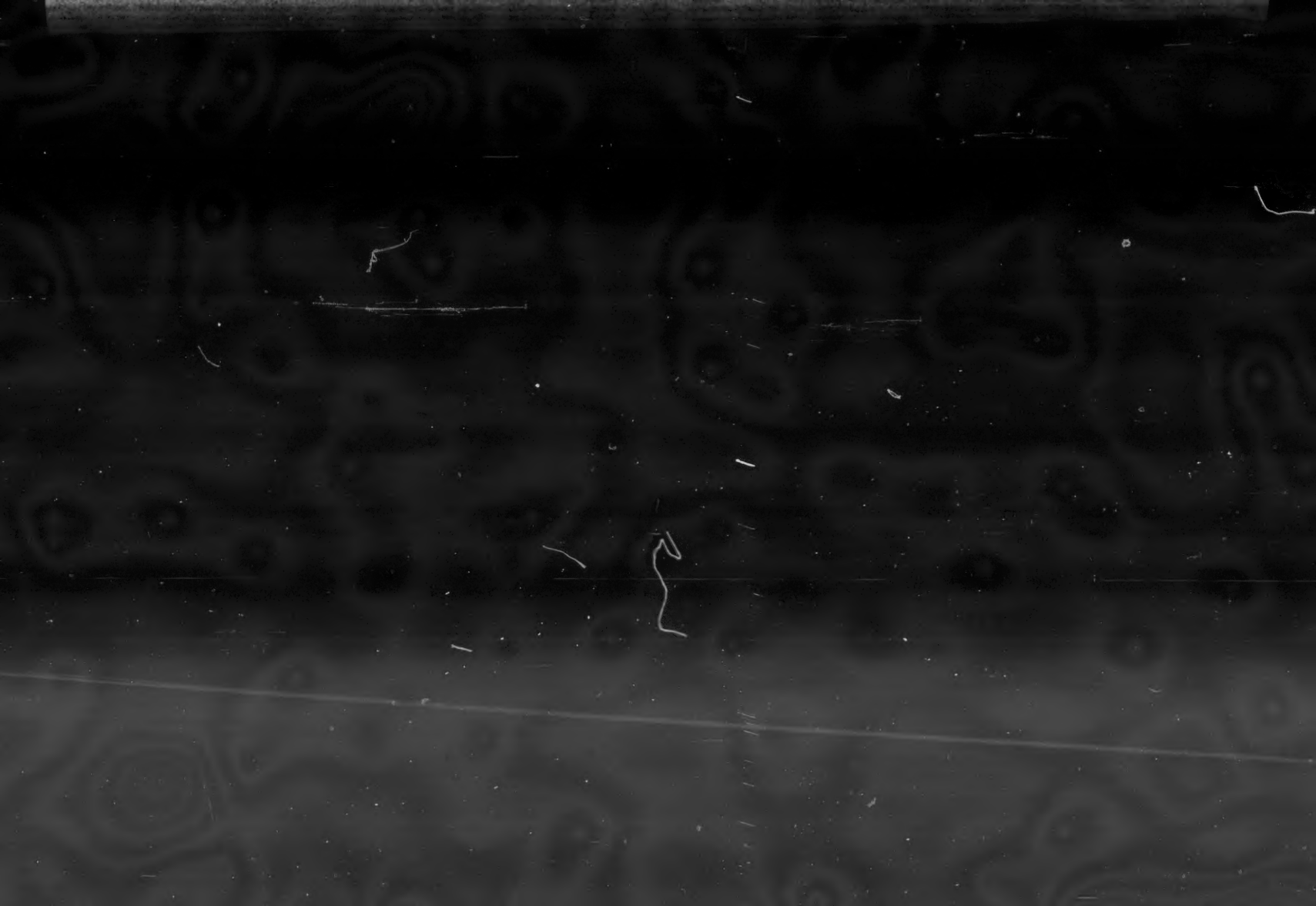
[23] MIKAYI, KÜCHI, and YASUI, KONO, On the gametophytes and embryo of *Pseudolarix*. Ann. Botany 25:639–647. *pl. 48*. 1911.

[24] DACHNOWSKI, ALFRED, A cedar bog in central Ohio. Ohio Naturalist 11:193–199. 1911.



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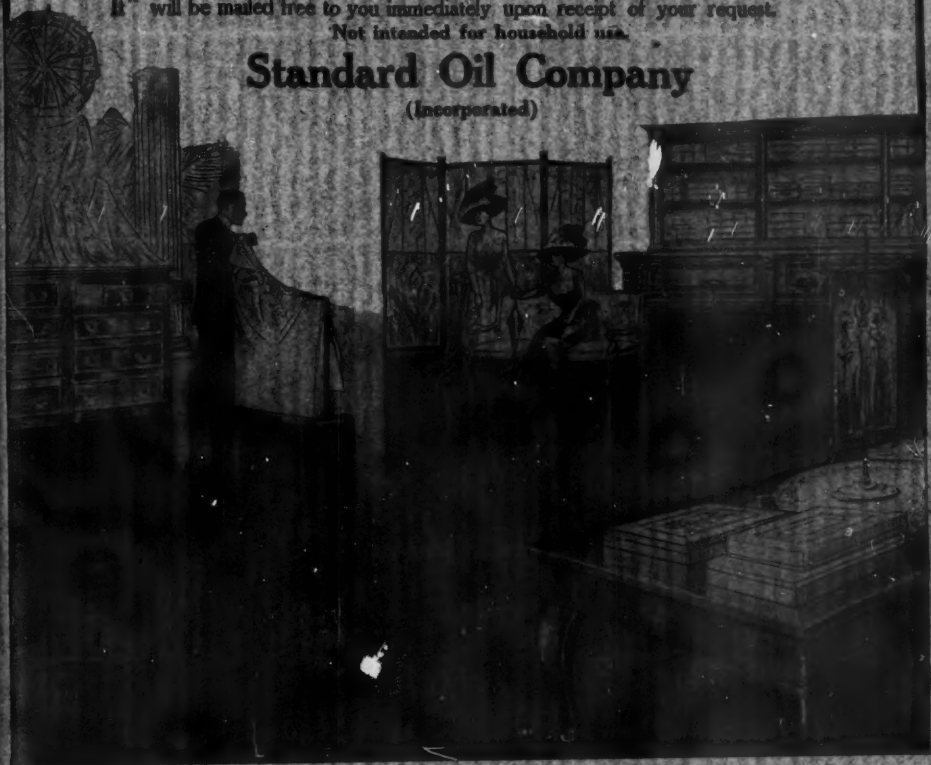

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